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# CONTRIBUTIONS IN SCIENCE

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# BIOLOGY AND DISTRIBUTION OF THE TIDEWATER GOBY, *EUCYCLOGOBIUS NEWBERRYI* (PISCES: GOBIIDAE) OF CALIFORNIA

CAMM C. SWIFT,[1] JACK L. NELSON,[2]
CAROLYN MASLOW,[3] AND THEODORE STEIN[4]

**ABSTRACT.** *Eucyclogobius newberryi*, the tidewater goby, is restricted to coastal, brackish-water habitats in California, originally from the mouth of the Smith River in Del Norte County, south to Agua Hedionda Lagoon, San Diego County. A southern Californian study population in Aliso Creek Lagoon, Orange County, has an annual life cycle entirely within the lagoon. Males dig vertical nesting burrows 10–20 cm deep in clean, coarse sand commencing in late April–early May at water temperatures of 18–22°C and salinities of 5–10‰. Adult males and females do not differ in length. During courtship, females have more striking breeding colors and display more aggressiveness than males. Females roam widely and court individual males that remain in or close to a nesting burrow. The male occupies an enlarged area of the burrow, where eggs hang from the ceiling and walls. Larvae hatch in 9–10 days at 5–7 mm and live in midwater about vegetation until 15–18 mm SL when they become benthic. Juvenile and adult fish feed visually from the substrate, primarily on ostracods, amphipods, snails, and chironomid larvae and pupae. Among California bay gobies, *Eucyclogobius* represents an extreme of small size, reduced squamation, short life span, low-salinity habitat, brief association with burrows, and only seasonally high aggression. The lack of a marine phase in the life history indicates that genetic exchange seldom occurs between separate lagoons. The present-day distribution may be a relict from an earlier period when brackish and/or estuarine conditions were more widespread and/or continuous. Low vagility, restricted habitat, and short life span make populations vulnerable to elimination by human activities and many populations have disappeared, particularly in southern California and in the San Francisco Bay area.

## INTRODUCTION

The tidewater goby, *Eucyclogobius newberryi* (Girard, 1857) (Fig. 1), has been poorly known because of its small size and restriction to brackish water habitats of coastal California. The species is of interest because of its narrow adaptation to brackish water, a rare condition among fishes, particularly on the west coast of North America. The disappearance of populations has begun to raise concern about the future of the species (Deacon et al., 1979; Potter, 1982; Ono et al., 1983). In this paper we describe the natural history of one southern Californian population, review the relevant literature, present the results of a field- and museum-collection survey for its occurrence, describe its behavior[5] in the field and laboratory, and discuss conservation strategies.

Previous work, including some of the early results of this study, is summarized by Moyle (1976) and Swift (1980). Tidewater gobies containing ovarian eggs in all months of the year were found in Aliso Creek Lagoon by Goldberg (1977). The distribution and seasonal occurrence of larvae of *Eucyclogobius* in Rodeo Lagoon (Fort Cronkite), Marin County, were studied by Wang (1982). Food habits and habitat requirements in San Antonio Creek, Santa Barbara County, based on quarterly samples were described by Irwin and Soltz (1984).

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[1] Section of Fishes, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

[2] Department of Biology, University of California, Santa Cruz, California (deceased).

[3] 817551 Minnehaha St., Granada Hills, California 91344.

[4] 523 N. Cliffwood, Los Angeles, California 90049.

[5] Observations on behavior were curtailed at the Aliso Creek site due to Nelson's then ongoing work. After his death his unpublished manuscript was made available. Since many of his findings confirm or extend Aliso Creek observations, they are here included, and Nelson is listed as a coauthor of this paper.

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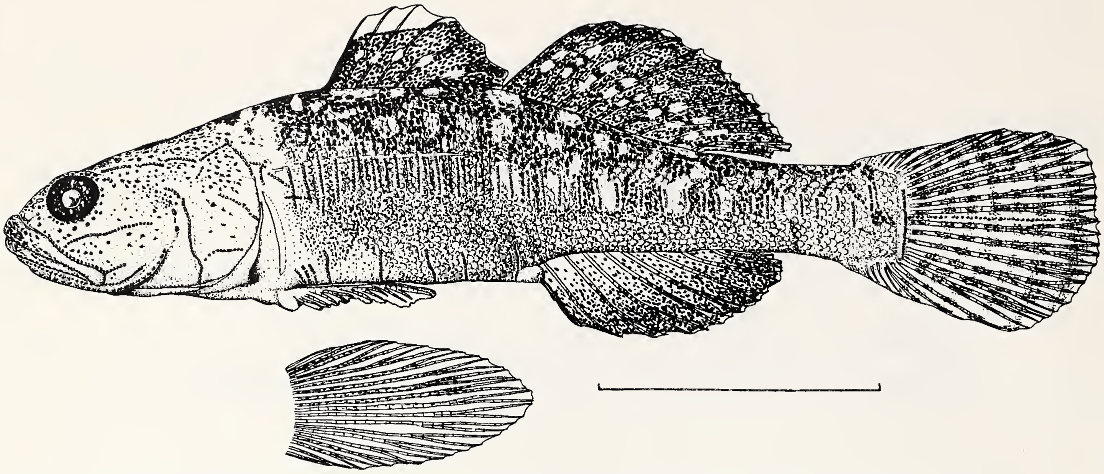

**Figure 1.** Female tidewater goby, from Aliso Creek Lagoon, LACM 42369-1, 33 mm SL, scale = 10 mm.

General natural history information appears in faunal works and other papers (Girard, 1857; Jordan, 1895; Jordan and Evermann, 1898; C.L. Hubbs, 1921, 1926; Dill and Shapovalov, 1939; Miller, 1939, 1943; Needham, 1940; C. Hubbs, 1947; Shapovalov and Taft, 1954; Hubbs and Miller, 1965; Eldridge and Bryan, 1972; Fierstine et al., 1973; MacDonald, 1977; Bell, 1978, 1979; Leidy, 1984; McGinnis, 1984).

The following errors in identification were discovered, based on examination of museum specimens (or the lack thereof) or on discrepancies in the original accounts. The account of *Eucyclogobius* by Carpelan (1961) was based on *Gillichthys mirabilis,* and the records for Carquinez Straits (Messersmith, 1966) are also misidentifications. Gravid *Gillichthys* from Mendocino County reported by Starks and Morris (1907) were based on *Eucyclogobius,* as was the record of *Gillichthys* from Waddell Creek (Snyder, 1938). The *Gillichthys* reported by Metz (1912) from Aliso Creek Lagoon in Orange County represent the population of tidewater gobies herein studied.

## METHODS AND MATERIALS

### TIME OF FIELD STUDY

Field observations were conducted at Aliso Creek from March 1973 to January 1977, but mostly from December 1973 to August 1975. The California coastline was surveyed for the species in 1970–1975, again in 1980–1982. Several biologists besides the authors provided information on localities during the study.

### COLLECTIONS

Museum collections canvassed include California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), Scripps Institution of Oceanography (SIO), University of Michigan Museum of Zoology (UMMZ), University of California, Los Angeles (UCLA), National Museum of Natural History (USNM), Moss Landing Marine Laboratory (ML), Humboldt State University, and Santa Barbara Museum of Natural History (SBMNH). Museum records, including specimens collected during our surveys, are listed in the Appendix.

Collections were made with small seines and dip nets; selected samples were preserved in 10% formalin and transferred after a week to 45% isopropynol or 70% ethanol.

### BEHAVIOR

Behavior was observed both in the field and in aquaria. Field observations were with the unaided eye, standing or sitting 1.5–5 m from fish in clear water up to 0.5 m deep. Observations in 1972 and 1973 in Waddell Creek and Bean Hollow lagoons, San Mateo and Santa Cruz counties, respectively, were made by Nelson. He made all laboratory observations presented in this paper on fish in aquaria 19 × 40 × 23 cm and 28 × 74 × 30 cm with water of 10‰ salinity at room temperatures of 21–25°C. Because of his death, many of Nelson's observations have not been confirmed. Details of some of his methods are lacking, and thus are distinguished in the results section.

### LIFE HISTORY

Length frequencies were taken from live individuals, most of which were returned to the lagoon. Standard length (to the nearest millimeter) and weight (to the nearest milligram) were taken on 3 December 1973 from live fish collected the previous day. Fish weighed were blotted dry, weighed fresh, preserved, and later sexed; all had empty digestive tracts. Otoliths and scales were examined for age marks; otoliths were treated with Beechwood Creosote (Sawyer, 1967) for examination whole under 50× magnification.

### FOOD

Diet was analyzed from the contents of the whole intestinal tract in three lots (37 specimens) of half-grown to adult fish. Most data are from fish taken in initial seine hauls from undisturbed areas. For each stomach, the volume of each individual food organism was visually estimated using 25× magnification. Food items were pooled for all fish from one locality and date.

## REPRODUCTIVE BIOLOGY

Fecundity was determined by complete counts of ovarian eggs, using fully gravid fish apparently full of yellow eggs that were mostly 0.5–1.0 mm in diameter. No size classes were apparent in these large eggs; smaller grayish, unyolked eggs 0.1–0.4 mm in diameter were not counted. In a few fish that apparently had already spawned, these smaller eggs predominated; these fish were not included in computations.

Embryonic development was described from live material collected in the gastrula stage and maintained in petri dishes until hatching. Post-hatching larvae were illustrated from preserved specimens collected in the lagoon.

The relationships between standard length and weight and between standard length and number of eggs were described with log-transformed variables (natural logs) in least squares and geometric mean regressions (Sokal and Rohlf, 1981).

## SALINITY

Salinity preference was determined by taking salinity data with collections, and salinity tolerance during three experiments conducted in a greenhouse from 10 February to 3 June 1975 at prevailing photoperiods in Los Angeles. Water temperatures ranged from 12.2 to 15.5°C. Test fish and controls were held in aerated 3.5-liter jars half-full of water. Fish were fed dry fish food every other day. Fish were observed twice a day for the first three or four days and daily thereafter, and dead fish were removed. Salt water was Instant Ocean sea salt diluted with deionized water, and all salinities (field and laboratory) were determined with an American Optical Company Refractometer accurate to 0.6‰. Fish were transferred directly from holding water into water at test salinities.

Experiment 1 on 10 February–7 March 1975 was with fish collected on 14 December 1974 and maintained in fresh water. Eight to 10 fish each were tested at 18.0, 35.4, 48.6, 60.0, 70.8, and 81.6‰; a control group remained in fresh water (1.8‰). Experiment 2, 20 March–11 April 1975, fish collected on 12 March in 13.2‰ were tested at 33.6, 44.4, 46.2, 49.2, and 55.2‰; a control group was held in fresh water (0‰). Experiment 3, 11 April–2 June 1975, utilized two groups of fish held at 13.2‰ since 12 March; a control group at 16.2‰ and test group at 40.2‰. Experiment 3 fish experienced a gradual increase in salinity due to evaporation.

## SAND PARTICLE SIZE

A sample of sand from the vicinity of breeding burrows was analyzed for particle-size distribution with a settling tube.

## ALISO CREEK STUDY AREA

Aliso Creek Lagoon (Fig. 2), where most of the field observations were conducted, is about 8 km SE of Laguna Beach on U.S. Hwy. 1, Orange County, California. It varies seasonally from 350 to 450 m by 10 to 20 m, and covers about 7500 $m^2$ (0.75 ha). Water depth is 1.5–2.0 m under the highway bridge and gradually shallows upstream. Most of the year the inlet stream is small ($\leq 0.03$ $m^3$/sec), but during winter runoff can flow up to 0.84 $m^3$/sec. In summer and fall runoff from a golf course and outflow from an Orange County Sanitation District Sewage Treatment Plant maintain some flow. Typically, the first winter rains (November to January) fill the lagoon to overflowing, breaking through the sandbar, emptying the lagoon, and leaving a sandy-bottom stream. Within a few days a bar builds up again at the mouth and at least a small lagoon quickly reforms. Several partial drainings and invasion of marine water may occur from December to March or April. Usually by April the lagoon closes to the sea. Inflow is balanced by evaporation and percolation through the sandbar, and only occasional waves from the highest tides wash over the barrier bar into the lagoon.

The bar and beach at the mouth and about 80% of the lagoon bottom are sand. The clean, light-colored sand bottom slowly accumulates a veneer of darker sediment. In the landward half of the lagoon the subsurface sand often turns black by midsummer with the buildup of hydrogen sulfide. Sand from the upper one-fourth of Aliso Creek Lagoon (in which several breeding burrows were discovered) was a well-winnowed coarse sand of relatively uniform size freshly washed during the previous winter (two particle-size analyses, mean diameter: 0.54, 0.58 mm; SD 0.81, 0.84; skewness, 0.30, 0.35; kurtosis, 2.77, 2.72). Under the highway bridge (20–40 m upstream of the mouth) and in the uppermost channelized portion of the lagoon, concrete boulders, rock, and gravel make up about 50% of the bottom. The bottom along the south shore is clay. Clay banks line both shores above the bridge, and concrete block (south) and conglomerate rock cliffs (north) line the shores below.

Upstream of the bridge, aquatic vegetation (*Typha*, *Scirpus*, *Salicornia*, and *Distichlis*) grows at the water's edge. *Ruppia* occurs in scattered patches on the bottom in shallow water. Small beds of a narrow-leaved species of *Potamogeton* develop in the middle and upper lagoon in the summer. Below the bridge, algae grow on the rocks. In late spring and summer, algal blooms often turn the water yellowish or greenish. Winter floods decimate aquatic vegetation, which begins reinvading in March or April.

The lagoon has both a longitudinal and vertical salinity gradient. Salinity is 0–10‰ at the upper end and near the surface, and 10‰ or more near the ocean and in deeper water. Stream water entering the lagoon is 1.8–2.4‰ due to effluent from a sewage treatment plant upstream. When swollen with winter rain, stream water is 0‰. From fresh or nearly fresh water in spring, salinity slowly increases until winter rain repeats the cycle.

Water temperature in the lagoon is about 15°C in the winter and up to 23°C in late summer. In winter marine water washing into the warmer lagoon, or stream water (8–9°C) cooled by low air temperatures, results in even

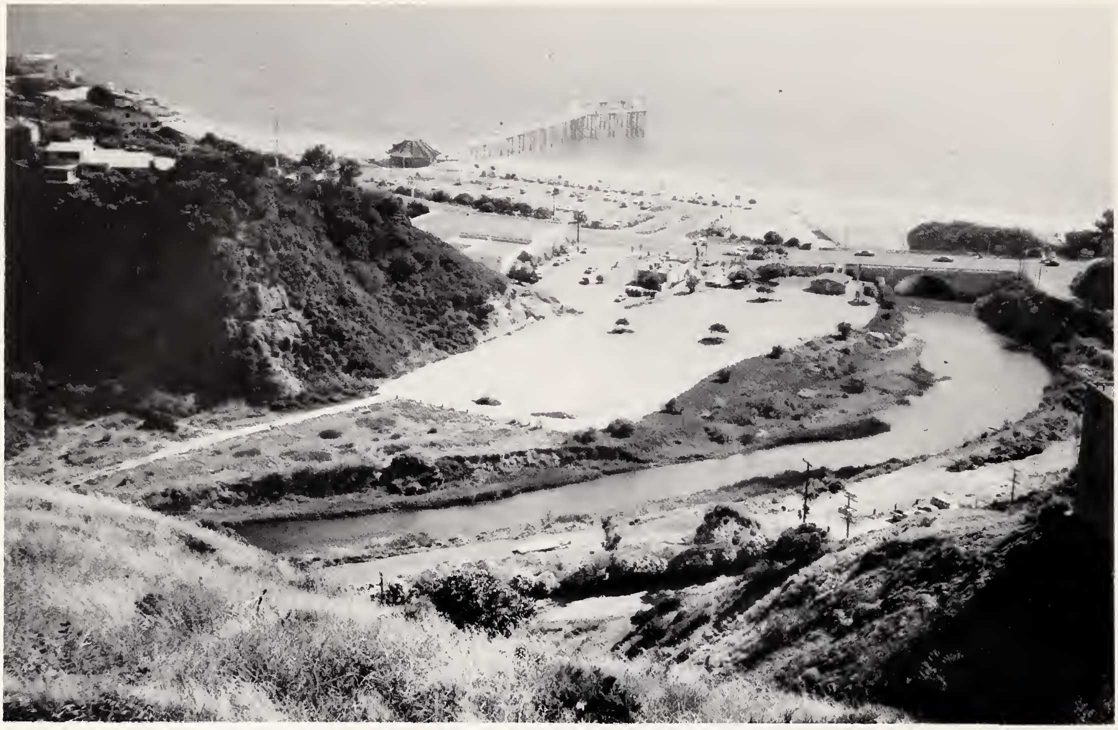

**Figure 2.** Aliso Creek Lagoon, Orange County, California, spring 1975.

cooler temperatures for short periods. In summer and fall the lagoon is usually cooler than the ocean and warmer than the stream by 3–4°C.

Similar seasonal cycles have been described for other lagoons in southern California (Carpelan, 1967), and for Lake Merced (Miller, 1958; Fahy, 1974), Waddell Creek Lagoon (Shapovalov and Taft, 1954), and Salinas River Lagoon (Hubbs, 1947; Smith, 1953) in central California, all of which historically held tidewater gobies.

## RESULTS

### AGE, GROWTH, RECRUITMENT, AND MORTALITY

No distinct annual markings could be found on otoliths or scales from 20 adult fish. Scales do not develop until fish are about two-thirds grown (25–30 mm SL). Then only those posterolaterally on the body grow large enough to overlap each other. Scales never develop anterodorsally or anteroventrally on the body.

Spawning commences in April or May at Aliso Creek and at Waddell and Bean Hollow lagoons. At this time only large adult fish were present at Aliso Creek. Several other museum collections taken in late spring before spawning begins also contain only large fish, despite the frequent abundance of small individuals into the winter (Fig. 3). Although length-frequency data (Fig. 3) appear to indicate that small individuals present in December 1973 grew into the younger of two size (age) classes in June, no small individuals were present during the observations on breeding behavior in April and May. Therefore the smaller class of fish sampled in June must be derived from the most recent spring spawning. The progression of this June peak through the summer indicates these early offspring predominate in the fall and winter population. Late summer and fall spawning was much less successful in 1974; fewer smaller individuals were present. Our data indicate that *Eucyclogobius* has an annual life cycle in southern California; specimens in museum collections suggest a similar pattern farther north (Fig. 4).

Considerable post-spawning mortality is indicated by a reduction in numbers of large individuals from midsummer onward, particularly males, and the frequent occurrence of emaciated and dead adults. Aquarium males fed little or not at all while guarding eggs and often appeared emaciated. Eggs take 9–11 days to hatch and with multiple clutches, males may go longer with minimal feeding. Females predominate in the sample of 3 December 1973, and female : male ratios from 16:1 to 3.1:1 cannot be rejected at the 0.01 level by the log-likelihood-ratio test (Sokal and Rohlf, 1981). Lengths of adult fish collected on 12 March 1975 (Fig. 5) did not differ significantly between sexes ($t = 1.498$, $df = 136$, $p = 0.2$) nor did the sex ratio deviate significantly from 1:1. Apparently older female fish die over the winter leaving the younger-year class with a 1:1 sex ratio.

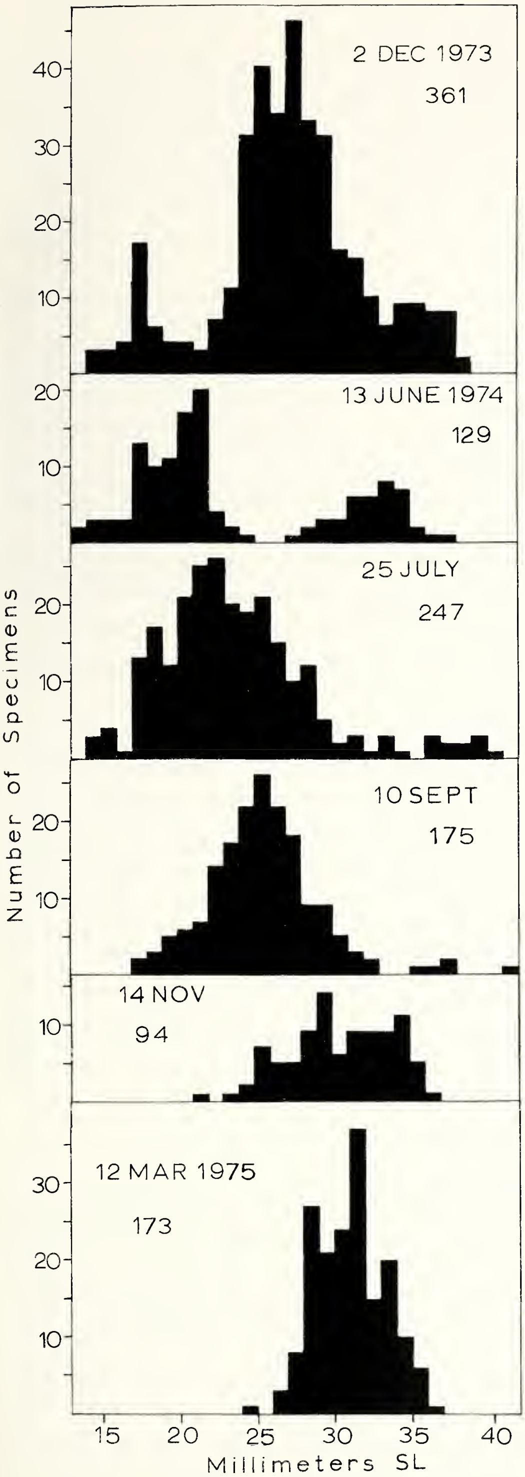

**Figure 3.** Length-frequency of successive collections of *Eucyclogobius newberryi* at Aliso Creek Lagoon, 1973–1975.

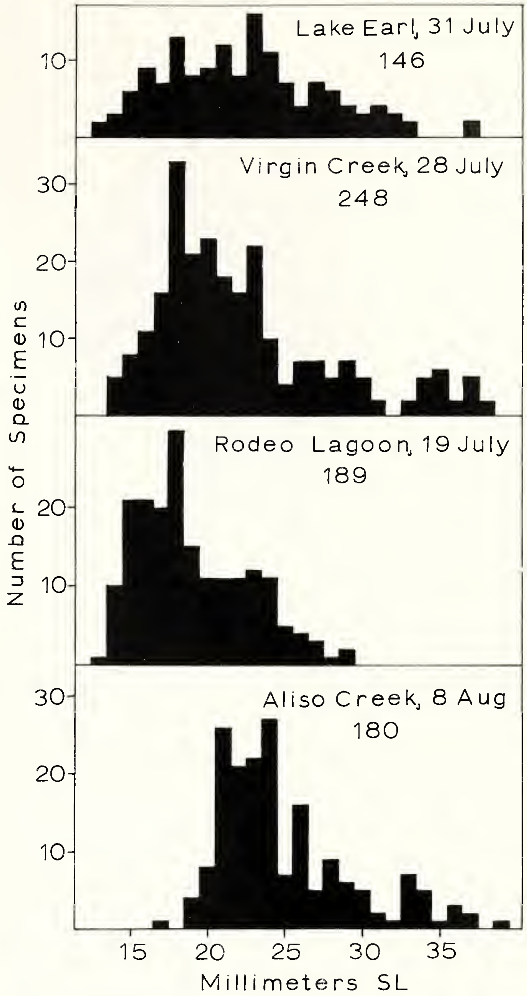

**Figure 4.** Length-frequency of four populations of tidewater goby, *Eucyclogobius newberryi*, summer 1975. Locality details in text. Localities arranged north to south. Rodeo Lagoon is in Capitola, Santa Cruz County, also known as Corcoran Lagoon.

## LENGTH AND WEIGHT

The length-weight relationships on 3 December 1975 for the Aliso Creek population as a whole, indicate that females are only slightly, and not significantly, heavier than males and no fish exceeded 1 g in weight (Table 1). There is little variability and narrow confidence limits because gonads were much reduced and stomachs empty. Gravid females are probably significantly heavier than males early in the breeding season.

## POPULATION SIZE

From late summer to early fall at Aliso Creek Lagoon, a few hundred gobies could be collected with a few sweeps of a small seine in most areas of the lagoon. Extrapolation to the whole lagoon indi-

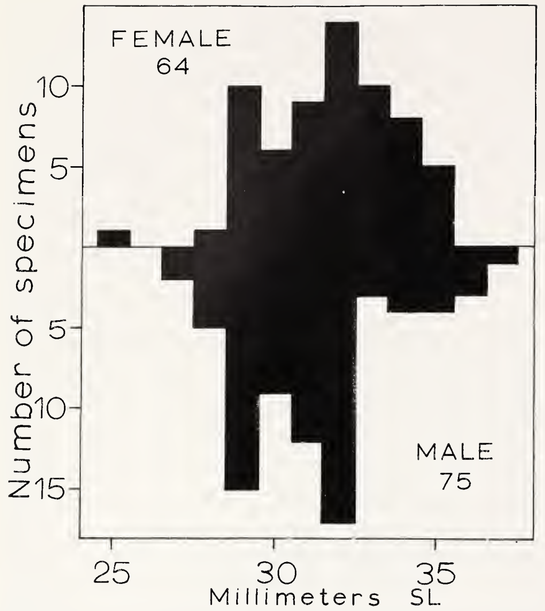

**Figure 5.** Length-frequency of male and female tidewater gobies from Aliso Creek Lagoon on 12 March 1975.

cates a population size of 10,000–15,000. In late winter and early spring before spawning occurs, equal collecting effort indicates a population size of 1000–1500 fish.

Aliso Creek Lagoon is about average size for coastal lagoons, but the extremes are considerable. Arroyo del Oso and Leffingwell creeks, San Luis Obispo County, are 10–30 m long and up to a few meters wide. Probably fewer than 100 fish overwinter in each of them. Fish are abundant at the few sample sites in Lake Earl (Del Norte County); with an area of about 1100 ha, it may contain a few million fish.

## FOOD

Half-grown to adult tidewater gobies were seen feeding on live animals on the surface of sandy or muddy substrate. Seventeen fish taken on 27 October 1973 at Aliso Creek contained 70% chironomid pupae by volume, 25% small invertebrate eggs, and 5% fragmentary algae. Ten fish (29–37 mm SL) collected on 13 June 1974 at Aliso Creek contained 4% snails, 60% ostracods, 30% chironomid larvae and pupae, and 6% amphipods. Eight of 10 specimens (29–39 mm SL) taken on 22 May 1970 at Jalama Creek, Santa Barbara County, contained food: 27% ostracods, 18% mayfly nymphs, and 55% chironomid larvae; two specimens were empty. In the fall of 1973, ostracods, amphipods, snails, and dipteran larvae were found in stomachs of 20 fish collected on 15 March 1973 from Waddell Creek. Fifty-seven ostracods (among 12 fish), 64 snails (among nine fish), and 14 dipteran larvae (among four fish) were tallied. Fish from San Antonio and Shuman lagoons, Santa Barbara County (Irwin and Soltz, 1984), contained ostracods, amphipods, chironomid larvae, and a minor contribution by aquatic insects and mysids.

## HABITS

Tidewater gobies occur on the substrate in loose aggregations of a few to several hundred individuals with no apparent size segregation. Fish move along the bottom in short spurts. Individuals occasionally hover in midwater along steep drop-offs or in dense aquatic vegetation. Except for adult males in the breeding season, fish do not burrow into the substrate in either nature or an aquarium. The escape mode is fleeing in long dashes (1–2 m) into deeper water or aquatic vegetation.

Tidewater gobies were typically abundant in shallow water ($\leq 1$ m deep), but deep water was seldom sampled. However, many smaller lagoons have little or no water deeper than 1 m.

## PREDATION

Two documented occurrences of predation on tidewater gobies are known. A 32-cm-TL *Salmo*

**Table 1. Least squares and geometric mean regressions of standard length and weight for *Eucyclogobius newberryi* collected on 2 December 1973. Log-transformed values are used, X = weight (centigrams); Y = length (mm).**

| Group | n | r | Least squares | Geometric mean | 95% Confidence interval for slope |
|---|---|---|---|---|---|
| Males | 42 | 0.9919 | $\ln X = 3.5183 \ln Y - 8.3859$<br>$\ln X = 0.27963 \ln X + 2.3996$ | $3.5471 \ln Y - 8.48317$<br>$0.28191 \ln X + 2.39154$ | 0.040616<br>0.040596 |
| Females | 93 | 0.9960 | $\ln X = 3.6159 \ln Y - 8.7461$<br>$\ln X = 0.27438 \ln X + 2.4262$ | $3.63028 \ln Y - 8.79438$<br>$0.27546 \ln X + 2.41992$ | 0.018604<br>0.018489 |
| All fish | 135 | 0.9952 | $\ln X = 3.6053 \ln Y - 8.7008$<br>$\ln Y = 0.27474 \ln X + 2.4224$ | $3.62244 \ln Y - 8.75861$<br>$0.27605 \ln X + 2.41787$ | 0.016729<br>0.016729 |

*gairdnerii* caught in upper Gaviota Creek Lagoon in August 1960 contained 6–10 gobies, about 75–100 mm TL (J. Radovich, pers. comm.); some or all of these may have been tidewater gobies. Sculpins (*Cottus*) have been observed to feed on *Eucyclogobius* in an aquarium (G. Barlow, pers. comm.).

## SALINITY RELATIONS

All sizes of tidewater gobies usually occur at the upper end of lagoons at salinities ≤10‰. Of 60 collections 39 were at 0–10‰, 12 at 10–20‰, 10 at 20–30‰, and one at 42‰, the last in Bennett Slough, a tributary of Elkhorn Slough, Monterey County. Records of ≤10‰ are given by Hubbs (1947) and Fierstine et al. (1973). Fish from 20–25 and 30‰ in Corcoran Lagoon, Santa Cruz County, are reported by Bell (1979). An adult specimen, CAS IX-24-1923 labeled Pebble Beach, Pescadero, California, may be from a marine habitat, from Pescadero Creek, or nearby Bean Hollow or Waddell Creek lagoons. Despite four years of extensive nearshore sampling for fish larvae off southern California (G. McGowen and M. Sowby, pers. comm.), the only marine records of larvae are two taken on 13 January 1980 in the vicinity of San Onofre Power Plant, San Diego County, immediately after heavy local runoff due to a large storm.

In the first salinity tolerance experiment (see Methods), all fish from 60.0, 70.8, and 81.6‰ expired in six hours; at 48.6‰ all fish expired in 24 hours. Those in fresh water (control), 18‰, and 35.4‰ all survived for 25 days.

In the second experiment, 80% of fish at 50.75‰ expired in 24 hours, and the two remaining fish died in nine days. All the fish at 45.5‰ died in six days, and 80–100% of the fish at 35.0, 36.75, and 40.25‰ survived 22 days, as did controls at 13.2‰.

In the third experiment, two groups of fish experienced a gradual rise in salinity due to evaporation for 53 days. One group began at 16.2‰, the other at 40.2‰. At the end, salinity was 25.2‰ and 61.8‰, respectively. Survival was 75% and 59%, respectively, with the die-off of fishes widely scattered over this time interval.

Experimental groups of fish in salinities above 41‰ experienced high mortality. In the third long experiment with slow change in salinity, over half the fish survived hypersaline conditions (up to 1.75 times that of seawater). Controls in fresh water survived up to 84 days from time of collection.

During winter rains and high flows of inlet streams, tidewater gobies can usually be collected a few tens of meters upstream in small creeks like Aliso Creek, and up to 1.5 to 2 km in larger streams like the Santa Clara, Ten Mile, and Smith rivers. In San Antonio Creek, Santa Barbara County, fish have been recorded up to 8 km inland (LACM records; Irwin and Soltz, 1984).

During summer algal blooms and when hydrogen sulfide ($H_2S$) builds up in the substrate, most fish are at the upper end where freshwater inflow exists or at the seaward end where occasional high-tide waves wash in from the ocean. Such summer restriction in habitat commonly occurs in disturbed and polluted lagoons. But in relatively undisturbed situations, fish remain scattered throughout, particularly over a sandy substrate.

## PARASITES

The only parasite noted on *Eucyclogobius* was the digenetic trematode *Cryptocotyle lingua*, which occurred on the skin of many adults from Corcoran Lagoon.

## LIVE COLOR

Nonbreeding life colors in juveniles and adults of both sexes are light semitranslucent gray, brown, or olive with black flecking and/or mottling. The dorsal, caudal, and anal fins are dusky, and the distal one-fifth or so of the spinous dorsal fin and a narrow distal edge of the soft dorsal and anal fins are cream, pale yellow, or pale orange. The body has few to many fine pearly white spots. Females often appear darker than males. At Aliso Creek, breeding males near burrows appear similar to nonbreeding individuals. In females the anterior half of the body and the spinous and soft dorsal fins, the anal fin, and the body between them often become strikingly black, except for a narrow distal edge of the fins which remains pale. The head, posterior, and tail body, remain similar in color to males. Much of this black pigment is lost in preservation.

Breeding females in central California are tan to reddish brown with a gold-brown to dark-brown area extending backward from the pectoral insertion to the vent. Melanophore patterns that change with behavior (dark-brown or black) overlying the yellowish abdomen may be responsible for observed variation in shades of gold to brown. Dorsal and anal fins are velvet black with white margins. The flanks of the females can become blue-black during bouts of aggressiveness. In central California, breeding males have a sooty-black head and body with small white spots on the dorsal and lateral surfaces. The dorsal and anal fins are sooty-black with a white margin. The dorsals also have small white spots. The caudal is translucent with five columns of white spots. In both males and females, the pelvics have a prominent elongate white spot and the pectorals are colorless.

## REPRODUCTIVE BIOLOGY

A genital papilla is present in both sexes, about four times larger in females than males (Fig. 6). Most

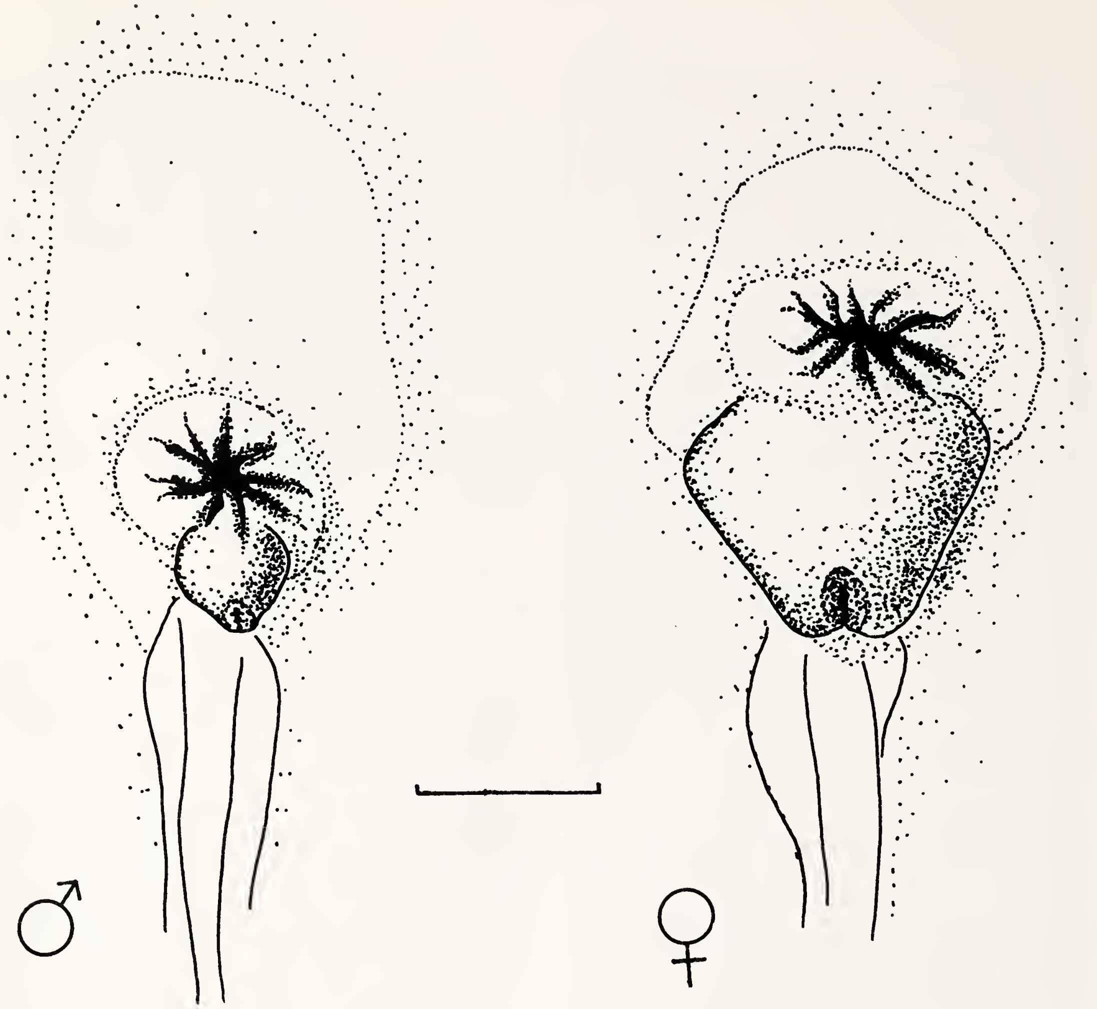

**Figure 6.** Ventral view of genital papillae of adult tidewater gobies, *Eucyclogobius newberryi* (LACM 42369-1, 34–35 mm SL. Anterior is up; scale = 1 mm.

fish over 25 mm SL can be sexed externally by this difference. Smaller papillae in nonbreeding individuals also exhibited a size differential between the sexes. Inactive gonads of both sexes are similar in size, but the testes were almost invariably half (and usually more) covered with black melanophores. Testes are 3–6 mm long, 1–2 mm wide, roughly triangular in cross section, and show little seasonal variation in size.

Ovarian eggs are spherical and up to 1.2 mm in diameter when mature. Counts of mature eggs range from 179 to 594 in fully gravid fish that lack smaller eggs. Egg number is related to length of the fish (Table 2, Fig. 7). Excluding the smallest fish, the lowest egg number was 272 for a fish 26.9 mm SL, probably about the minimum size for sexual maturity in females.

The vitelline membrane becomes elongate and pear-shaped after fertilization, essentially identical to that of the eggs of *Typhlogobius californiensis* (Eigenmann, 1892; Breder, 1943) and *Gillichthys mirabillis* (Weisel, 1947). The fertilized ova are pale iridescent yellow with a cluster of 15–20 small oil droplets against one side. The yolk is 1.5–1.7 mm in diameter, and the vitelline membrane is 2 mm wide and 5–6 mm long. The eggs are attached by the pointed ends to sand grains lining the burrow.

Hatching of eggs from nests in the wild from central California took nine days at 21–25°C. Eggs collected from Aliso Creek had the blastodisc developed, and it encircled about one-third of the yolk. About 30 such eggs held in the laboratory at 18–21°C hatched in 9–10 days. By the second day the body was elongate with otic cups and lens vesicles visible. Flexing of the body was noted on the third day, and the heart beat began on the fifth day.

Larvae hatched in the laboratory are 5–6 mm long; 6–7-mm-SL and larger larvae are commonly collected free-living in lagoon vegetation (Fig. 8). Six-millimeter larvae had complete median fin folds, small, paddle-like pectorals, and no visible sign of pelvic fins. The air bladder is a simple longitudinal oval. A longitudinal series of stellate melanophores forms thin dorsal and ventral median black lines with many fine lateral processes (Fig. 8A). One to three melanophores occur at each jaw articulation. A small patch of cells lies at the base of the caudal fin fold. At 8–9 mm many fin rays are ossified, but the fin folds are still low and rounded (Fig. 8B); a few melanophores appear on the head and posteriorly on the body, a pelvic fin bud develops, a dark patch of melanophores is present immediately posterior to the anus and hindgut, and the air bladder is more elongate. At 11–12 mm SL the dorsal, anal, and caudal fins have a full complement of fin rays (Fig. 8C). Melanophores have migrated out onto the caudal rays, and many more are on the head and body. The distinctive middorsal and midventral lines give way to the mottled adult pattern. Complete development of the pelvic fins (and attainment of the juvenile stage) takes place at 16–18 mm SL. Fish orient largely to the substrate at this time.

At Aliso Creek, breeding commenced in late April 1974 in the upper end of the lagoon. Water temperature was 18–19°C and salinity was low, but not recorded. About 30 burrows were found on 28 April 1974, concentrated on a sand shoal 3 m long, 0.5 m wide, and in an 11-m linear series parallel to one steep, north-facing shoreline. The shoreline entered the water at about a 45° angle. The burrow entrances, as those on the sandbar, all were 24–30 cm deep. At Bean Hollow Lagoon, the burrows found were restricted to a 4-m² area of sandy mud. The entrances of the more or less vertical burrows at Aliso Creek were surrounded by a rounded area of cream or yellowish sand (42–160 mm diameter, n = 26, x = 72.3) that contrasted with the darker adjacent undisturbed sand. Distances between the edges of the clear sandy areas ranged from 50 to 550 mm (n = 22, x = 143.5). Hand excavation of seven burrows revealed either a male (three burrows) or a male and female (four burrows) 75–100 mm below the surface. A clump of about 50 eggs was found with one pair.

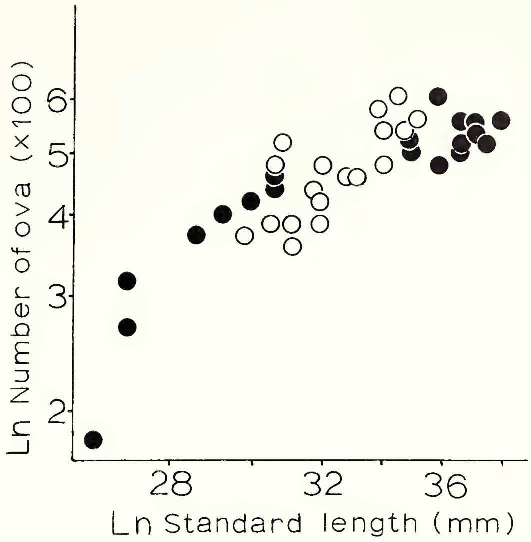

**Figure 7.** Log-log plot of number of eggs versus standard length in female *Eucyclogobius newberryi* (n = 38). Open circles are Aliso Creek fish (LACM 35814-3, 21 January 1973, and 42369-1, 13 June 1974). Black dots are fish from Oak Knoll Creek, San Luis Obispo County (LACM 1007, 3 May 1958).

Male fish occupied several of the clear areas around the burrow entrances at Aliso Creek Lagoon. Two males at separate burrows entered head first. Slowly and laboriously undulating the body in a backward-swimming motion, they emerged tail first and dropped a mouthful of sand within 100 mm or so of the entrance. On 13 June the clear areas were not evident. One male excavated a burrow for about half an hour, completely disappearing 10–12 times for 10–20 seconds each. He was distracted by female fish five or six times, and once by a half-grown *Gambusia*. Subsequently the male moved 80–100 cm away, but returned in 10 minutes. In the next hour he removed mouthfuls of black sand five or six times.

At midday on 28 April, female fish (black coloration described above) often swam in midwater over the burrows. Several times females displayed to each other by maximally expanding the median fins while lined up in opposite directions side-to-

**Table 2. Least squares and geometric mean regressions of standard length and number of mature ova using log-transformed data. X = standard length; Y = number of ova.**

| Site | n | r | Least squares | Geometric mean | 95% Confidence limit for slope |
|---|---|---|---|---|---|
| Aliso Creek | 18 | 0.7886 | $\ln X = 0.24382 \ln Y + 1.9888$<br>$\ln Y = 2.5504 \ln Y - 2.7536$ | $0.30916 \ln Y + 1.58825$<br>$3.2346 \ln X - 5.13732$ | 0.325977<br>0.3259432 |
| Oak Knoll Creek | 20 | 0.8873 | $\ln X = 0.39437 \ln Y + 1.0971$<br>$\ln Y = 1.9962 \ln X - 0.89316$ | $0.44447 \ln Y + 0.79168$<br>$2.24986 \ln X - 1.78117$ | 0.2284734<br>0.228399 |
| Both combined | 38 | 0.8517 | $\ln X = 0.35803 \ln Y + 1.3044$<br>$\ln Y = 2.0259 \ln X - 0.96366$ | $0.42040 \ln Y + 0.502708$<br>$2.37868 \ln X - 2.19578$ | 0.1771222<br>0.1632797 |

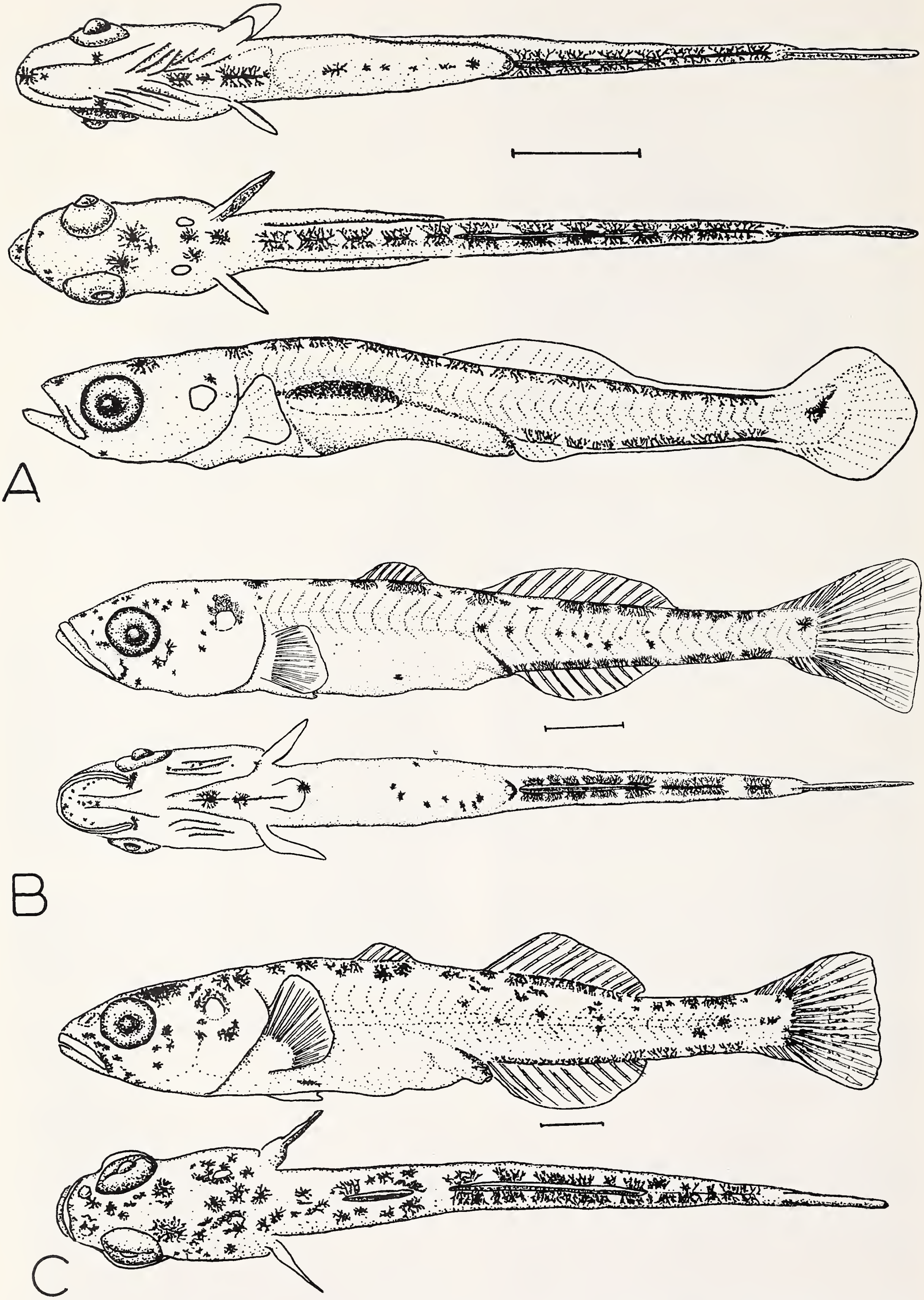

Figure 8. Larvae of tidewater goby, *Eucyclogobius newberryi* from Aliso Creek Lagoon, LACM 43748-1, collected on 22 May 1976. **A.** 6 mm SL; **B.** 9 mm SL; **C.** 11.5 mm SL. Scales = 1 mm.

side about 10–15 mm apart. Usually these encounters were near burrow entrances, and on two occasions the "winner" of such face-offs proceeded to enter the burrow with the male fish for several minutes. In a third episode, the second female fish followed the first into the burrow, but one female re-emerged after a few seconds and left the area.

Breeding males from central California observed in an aquarium pressed the sides of the head against the substrate, raised up the caudal end, and drove themselves head first into the substrate with vigorous swimming motions. They turned and undulated to the surface along the same path. The males deepened and widened the burrow, removing sand with the mouth until a small mound of fresh substrate surrounded the burrow entrance.

Central Californian males in an aquarium attempted to burrow into gravel and mud substrates about 4 cm. In coarse aquarium gravel the burrow collapsed, but the male continued to attempt burrow construction for four days. In substrate from Waddell Lagoon, a male dug a burrow next to the aquarium glass in two hours. Mucus was found on both gravel and mud-sand mixtures, indicting that body mucus cements and supports the burrows.

Central Californian males also rearranged the interior of their burrows and changed the entrance location. The entrance was closed by spitting a sand-mucus plug into the opening and reopening the burrow some distance away. In the laboratory, male fish closed the entrance to their burrows only from the inside. If the male was feeding or in the burrow with a female, the entrance remained open.

Closure made nests difficult to locate in the field; the substrate accumulated near the burrow entrance soon became inconspicuous. Ripe females appeared to have little trouble locating nest sites, conspicuous or not.

Female fish were often noted seeking out and courting males at the burrows. After a female begins courting, the male may blow a sand plug into the entrance. He may pop open the burrow entrance, exit, and line up parallel with the female. He may swim about the entrance with her, undulate his body, and exchange tail slaps. The male might then stop, rest with his head pressed to the substrate next to the burrow, and suddenly dart into the hole, soon followed by the female. Or he may dive inside and blow a sand plug or otherwise obstruct the burrow's entrance to the female. Of 23 courtships lasting more than two minutes (Bean Hollow, 3 July 1973), only one led to a female successfully entering a male's burrow. In the remaining 22 the male left his nest only five times. On 17 occasions the male either: (1) opened the entrance, poked his head out briefly, and then retreated and remained quiet; or (2) resealed the entrance. Laboratory behavior of male fish was essentially the same.

Egg laying was observed in a burrow next to the glass wall of an aquarium. The male remained close to the female as she suspended her eggs, one by one, from the roof and sides of the burrow. Occasionally the male rapidly undulated back and forth, rotating along his long axis while moving slowly within the nest, presumably releasing milt. Egg laying lasted one hour and 47 minutes. The female then left the burrow. The male did not fan or otherwise manipulate the eggs, but they appeared clean for five days. Then the male piled mud next to the glass, occluding further view. It is not known if the eggs were fertile or if they hatched, since no fry appeared in the aquarium. Eggs were found in varying states of development in individual burrows in the field in central California. Thus, males probably mate with more than one female.

Males were not very aggressive, and laboratory and field interactions between males were few. After constructing a burrow, they seldom ventured out during the day. When out, males occasionally reacted to one another by biting at the substrate, head-standing with the chin close to the ground, and curving the tail up over the body, undulating laterally. Rarely, males lined up parallel to one another and delivered blows using the caudal fin and posterior end of the body. In the field, males were observed to come close to each other without combat. In only one instance did one male enter another's burrow without interference from the presumed owner. In the laboratory, males often attacked other males that attempted to enter their nests.

Laboratory observations indicated that females can influence a male building its nest. On two occasions, males digging at one site moved due to the activity of a female. Each time, the female approached the male, swam excitedly around him, moved nearby, and assumed a pre-digging stance (head pressed to the surface and tail raised off the substrate). On one occasion the female took mouthfuls of substrate and pushed her head into the substrate. On both occasions the male fish stopped digging at the original site, joined the female at the new location, and dug a successful burrow.

Ripe, sexually active females were aggressive. In the field and laboratory they attacked other ripe female fish. Females bit the substrate, aligned themselves parallel to one another, and exchanged tail slaps. When parallel or when approaching another individual, the aggressive female swam in a stiff posture with the dorsal, ventral, and caudal fins fully erected and usually resting on the tips of the extended pelvic fins. Female fish occasionally bit each other, and their aggression was more frequent and intense than that of the males. At Bean Hollow, only one instance of male-male aggression was observed, and none was observed at Waddell Lagoon. We witnessed 108 and 17 female-female aggressive interactions, respectively, at these sites during 60 minutes of observations at each location. However,

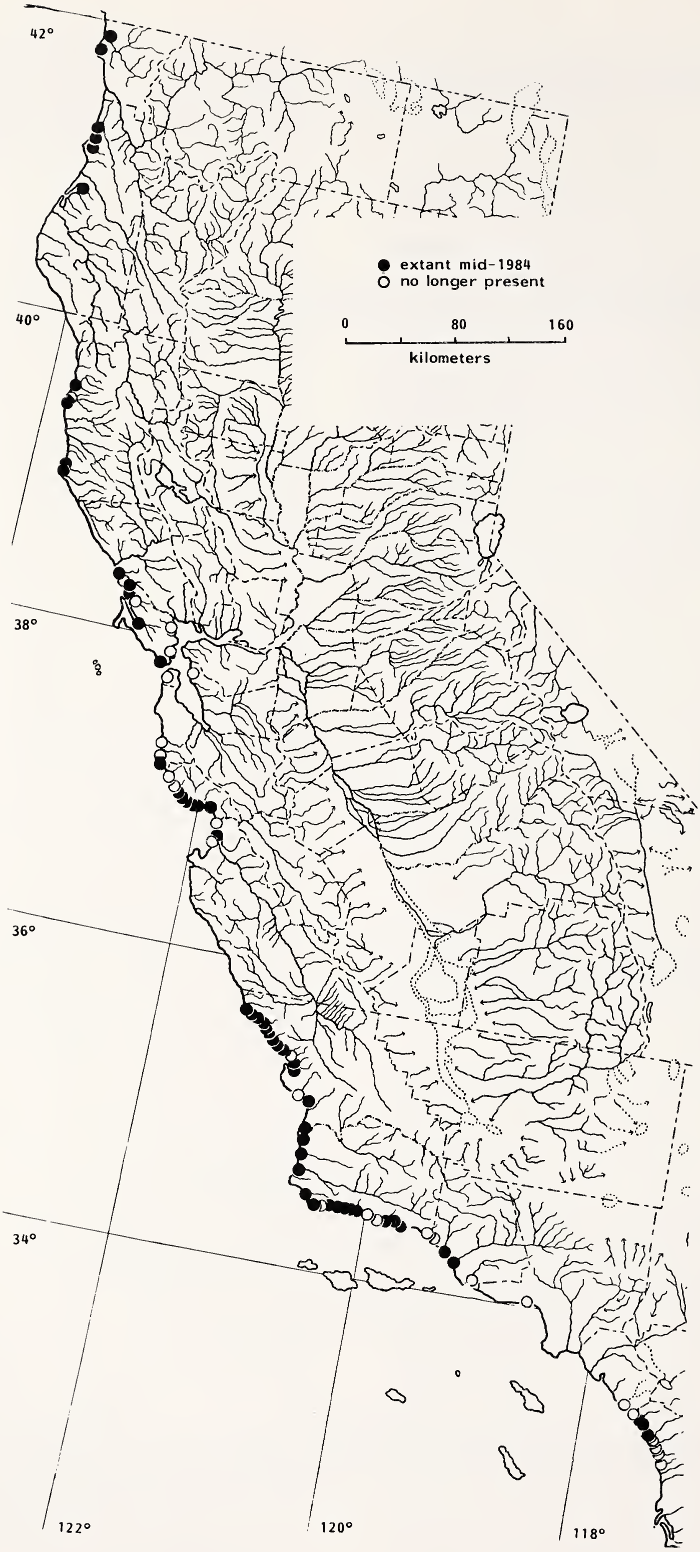

Figure 9. Distribution of the tidewater goby, *Eucyclogobius newberryi.* Solid circles represent populations viable in 1984, open circles represent museum records for localities where fish can no longer be found. In cases of close overlap, not all localities are plotted.

since males are seldom out of their burrows once the reproductive season begins, chance encounters between them are less frequent.

In the laboratory, female gobies established a social hierarchy. One female always displaced all other females in a given aquarium when they approached burrow sites. On a few occasions when nesting males chased other female fish, the dominant female placed herself between the male and the other female. The dominant female then nudged and swam about the male attempting to lead him back to his burrow. The number of egg clutches laid during the study indicated that many unwitnessed breedings occurred. Some of these may have involved subordinate females. All seven observed breedings (the female is allowed to enter the burrow) involved the high-ranking female.

In the field one female does not control access to all males. Rather, individual females assumed temporary dominance at single burrow sites. Successful females remained near a burrow for 30 minutes, occasionally longer. If unsuccessful after courting a male fish for some time, the female swam away or another female displaced the originally dominant fish. The single successful courtship witnessed in the field involved a female that was dominant at the time in the area.

Initially a ripe female entered a nesting area and swam slowly over the substrate. She settled to the bottom and placed her lower jaw on the substrate, or rested with her fins spread and hopped in a tight circle around an area of sand. Usually a hole appeared in the substrate, and a male extended its head out into the open. Occasionally the only evidence of the male's presence was a rhythmic rise and fall of the substrate.

Once the male was visible, the female began swimming about the opening. She erected her dorsal and ventral fins maximally and hopped and dashed around the circumference of the aperture. Violent undulations of the body often occurred at this time, and the female often bumped the male's head with her caudal fin or vent areas. She sometimes rested over the opening of the nest with her vent exposed to the male below or cupped the head of the male with the posterior end of her body. Many of these motor patterns were also observed in female-female aggression. However, the female never rushed at the male or bit or tail-slapped the male as much as she did another female. After a period of such activity, the male often allowed the female to enter its burrow. Not all courtships succeed, and some breedings occur without a courtship period.

Courtship activity usually led to some female-female aggression in both the laboratory and the field. If a female started to court a nesting male, other females were attracted. Melees of up to six females occurred. During 23 courtships observed at Bean Hollow on 3 July 1973, 18 were interrupted by one or more interloping female fish. All observed laboratory courtships were interfered with (n = 75), but the dominant female successfully defended the nest sites.

In the field, turnover of females could seldom be assessed without individual marks. However, on a few occasions where differences could be discriminated among the females, dominant females were displaced. In the laboratory, a few colorful females reverted to the olive-tan nonbreeding colors and were able to approach nesting males closely. Only an hour previously, they had been attacked by the dominant female. None of these reverted fish entered a burrow.

## DISTRIBUTION

The distribution of the tidewater goby is from Tillas Slough (mouth of Smith River), Del Norte County, south to Agua Hedionda Lagoon, San Diego County, California (Fig. 9). These localities correspond almost exactly to coastal regions with littoral cells of sediment movement (Habel and Armstrong, 1977) that facilitate lagoon formation. It is apparently absent: (1) between Humboldt Bay and Ten Mile River, (2) between Point Arena and Salmon Creek, and (3) between Monterey Bay and Arroyo del Oso (about 3 km north of Piedras Blancas Light). The coastline is steep in these areas and lagoons are usually absent. Museum records exist for 87 localities as of mid-1984 and are listed in the Appendix. About 40 additional coastal streams and lagoons have been collected and appear suitable for the species, but no *Eucyclogobius* have ever been taken. Nine are so large that a small population of tidewater gobies could exist undetected, namely in the Klamath, Eel, Mattole, Noyo, Albion, Navarro, Garcia, Gualala, and Russian rivers.

## ASSOCIATED FISHES

South of Point Conception, native species often collected with tidewater gobies are *Leptocottus armatus, Fundulus parvipinnis, Atherinops affinis, Platichthys stellatus, Hypsopsetta guttulata, Gila orcutti, Gasterosteus aculeatus,* and *Salmo gairdnerii.* North of Point Conception these species (except *Fundulus* and *Gila*) occurred, and *Cottus asper* is also common. In the Salinas River Lagoon Hubbs (1947) also collected *Catostomus miniotiltus* (= *C. occidentalis*), *Orthodon microlepidotus, Rhinichthys osculus, Ptychocheilus grandis, Cyprinus carpio,* and *Archoplites interruptus* with *Eucyclogobius.* In a few larger lagoons both north and south, *Cymatogaster aggregata* and *Syngnathus* sp. occurred. Adult *Leuresthes tenuis* were occasionally taken in Aliso Creek Lagoon (at salinities of 6–7.2‰) in the summer, probably carried in by waves during the fish's nocturnal spawning. The introduced mosquitofish, *Gambusia affinis,* almost invariably occurred with *Eucyclogobius* in coastal lagoons south of Point Conception but was usually absent from strictly coastal localities farther north.

## DISCUSSION

On the Pacific coast of the United States the tidewater goby is almost unique among fishes in its restriction to low-salinity water. The brackish region of lagoons and/or estuaries in general contains few endemic organisms; through time few species have adapted exclusively to this habitat (Haedrich, 1983; Hedgpeth, 1983). The only other brackish-water species in California are *Hypomesus transpacificus* and *Pogonichthys microlepidotus* (Daniels and Moyle, 1983) known only from tidal fresh and brackish waters of the Sacramento–San Joaquin Delta. *Eucyclogobius* is at the freshwater end of an ecological series (based on salinity) of phyletically related eastern Pacific temperate bay gobies (Ginsburg, 1945; Birdsong et al., 1988). Marine species are *Lepidogobius lepidus, Typhlogobius californiensis,* and *Lethops connectens.* Mostly estuarine are *Ilypnus gilberti, Quietula y-cauda,* and *Clevelandia ios.* Often occurring in low-salinity or fresh water are *Gillichthys mirabilis* and *Eucyclogobius newberryi.* However, *Gillichthys* also often occurs in hypersaline conditions (Barlow, 1961a, 1961b, 1963), and is known from the widest range of salinities (Moyle, 1976). However, *Gillichthys* can survive only about two weeks in fresh water (Barlow, 1961a), whereas *Eucyclogobius* has survived at least 84 days.

The biology of *Eucyclogobius* corresponds to one of two life history tactics proposed by Grossman (1979) for north temperate gobies, namely a combination of small size, short life span, and an annual life cycle, possibly with multiple reproductions per season. Young-of-the-year were collected by us from May to December at Aliso Creek, and by Wang (1982) in Rodeo Lagoon, Marin County. However, Goldberg (1977) found at least some females with mature eggs in all months (April 1974–April 1975) at Aliso Creek. He concluded that the capability for year-round spawning exists. Females in the 2 December 1974 collection (Fig. 3) have much reduced gonads (compared with April or May specimens), but some did contain a number of mature eggs. The potential for year-round spawning exists but probably is seldom, if ever, realized because of low temperatures and disruption of lagoons by winter rains.

The breeding behavior of the tidewater goby is noteworthy in the dominance and aggressiveness of female fish accompanied by their more striking, mostly black, breeding colors. This behavior is the opposite of the situation in most gobies (P.J. Miller, 1984), and for that matter most fishes (Potts, 1984; Potts and Wootton, 1984). However, black breeding colors are found in many male gobies (Miller, 1984). The aggressiveness of females is most pronounced in the confines of aquaria; it was more limited in the field. Much less interaction was noted between males, possibly because burrows were already established.

Considerable intraspecific aggression between individuals of burrow-inhabiting California gobies has been documented in laboratory-held *Lepidogobius lepidus* (Grossman, 1980), *Typhlogobius californienis* (MacGinitie and MacGinitie, 1968), and *Gillichthys mirabilis* (Weisel, 1947). Weisel (1947) also noted considerable blackening of body and fins, both in a dominant nesting male and other mature fish of both sexes. The color was transitory and elicited during aggressive bouts. *Eucyclogobius* falls at the lower extreme in aggressivness among these species and lacks territoriality during the nonbreeding season.

In *Eucyclogobius,* only the male burrows and only in the breeding season, mostly and perhaps exclusively in coarse sand. Some Californian bay gobies (*Gillichthys, Lepidogobius, Typhlogobius,* and *Clevelandia*) use the burrows of invertebrates (Ricketts et al., 1985). Hoffman (1981) showed that *Clevelandia* was not as strongly dependent on invertebrate burrows as was formerly believed. *Ilypnus gilberti* and *Quietula y-cauda* also build burrows in finer sand and/or mud in bays (Brothers, 1975). Such burrows may provide protection from the predation pressure on bay gobies documented by MacGinitie and MacGinitie (1968) and Horn (1980). The brackish habitat of *Eucyclogobius* lacks commensal burrowing organisms, and aquatic predators appear far fewer. Lack of tidal fluctuation also obviates the need for a retreat at low tide.

Predation on *Eucyclogobius* is virtually undocumented, but a variety of native bird and a few fish predators (*Leptocottus armatus, Cottus asper, Salmo gairdnerii*) occur in coastal lagoons. Smaller fishes like mosquitofish (at least in southern California) and stickleback could prey heavily on young gobies. Individual females with dark breeding colors often are obvious in spring and early summer, but the color (not present in preserved specimens) can be altered considerably in a few minutes. This ability obviously reduces the period of vulnerability to visual predators.

More native predatory fishes occur in the San Francisco and Monterey bay drainages. *Archoplites interruptus* (Centrarchidae) and *Hysterocarpus traski* (Embiotocidae) were widespread in the delta and many tributaries of the bay. Subsequently, several exotic centrarchid species and the striped bass, *Morone saxatilis,* were introduced into San Francisco Bay tributaries. The three San Francisco Bay records of tidewater gobies are all seaward of the major tributaries of the bay where these predators occur. Hubbs (1947) reported collecting *Archoplites* (possibly introduced) and *Eucyclogobius* together in the lower Salinas River in August 1946, and the last known collection of *Eucyclogobius* from there was taken in 1951. Six coastal lagoons contain centrarchids but lack *Eucyclogobius:* Lake Cleone, Mendocino County; Abbott's Lagoon, Marin County; Oso Flaco Lake, San Luis Obispo

County; Lake Merced, San Francisco County; and Buena Vista and Agua Hedionda lagoons, San Diego County. The latter three historically contained tidewater gobies. Many small *Lepomis cyanellus* were taken with *Eucyclogobius* on 21 January 1973 at Aliso Creek Lagoon. *Lepomis* were never taken again. Otherwise centrarchids and tidewater gobies have not been taken together and perhaps cannot coexist.

A black pigmentary investment on the testes, as in mature *Eucyclogobius*, is rare in vertebrates. Specimens of related bay gobies (LACM) show it well developed in *Ilypnus gilberti*, variably developed in *Clevelandia ios*, and absent in *Gillichthys mirabilis, Quietula y-cauda, Q. guaymasiae, Lepidogobius lepidus, Typhlogobius californiensis*, and *Lethops connectens*. Otherwise it is unrecorded in gobies (Miller, 1984) and in most other fishes as well (Nagahama, 1983). Wootton (1976) notes its occurrence in *Gasterosteus aculeatus*. It rarely occurs in lizards and mammals, and two alternative (but unproven) functions are postulated (Guillette et al., 1983): (1) to absorb solar radiation and thereby protect the testis from damage, or (2) to warm the testis with absorption of solar radiation. Since any warming would be quickly dissipated in water, the protective function only should be pertinent to fishes.

Precipitous coastlines where lagoons do not form at stream mouths define three presumably natural gaps in distribution noted previously. The Los Angeles Plains area of southern California (Culver and Hubbs, 1917) is a fourth hiatus not explainable by steep shorelines. No specimens exist to verify early published records from San Pedro and artesian wells in Santa Monica (Eigenmann and Eigenmann, 1892). This break also exists in the distribution of the freshwater *Gasterosteus aculeatus microcephalus;* only *G. a. williamsoni*, another freshwater stickleback, occurred on the Los Angeles Plain (Miller and Hubbs, 1969). Given extensive habitat modification and few early fish collections, some credence can be given to each of the four scenarios possibly involving *Eucyclogobius* and *G. a. microcephalus:* (1) both existed on the plain and disappeared, either historically or prehistorically; (2) and (3) only one or the other occurred and disappeared; or (4) neither ever lived in the area. The habitat must have been ideal for both taxa, and the negative evidence of lack of collections is not a strong argument against their original presence. Bell (1978) also discussed the equivocal nature of negative historical data in records of southern California freshwater fishes.

Barlow (1963) suspected that populations of *Eucyclogobius* were somewhat isolated from each other. Genetic differentiation between populations (Crabtree, 1985) supports the idea that interchange between populations is restricted. Our life history data also indicate that the complete life cycle is spent in lagoons or upper bays. Larvae provide at least a possibility of dispersal, but in San Francisco Bay and southern California, where many populations have disappeared, no case of recolonization is known. Today, populations are separated more widely, further isolating them. Brackish-water animals often show more morphological variability than freshwater or marine ones (Rasmussen, 1973; Wolff, 1983), perhaps due to such isolation.

The present distribution of *Eucyclogobius* may be a relict one from a time when brackish-water conditions were more widespread. Such distribution of several gobies in Mediterranean brackish coastal lagoons has been explained by alternating Pleistocene incursions of fresh and brackish water from the east (Zenkevitch, 1963; Miller, 1973). These taxa provide the closest ecological analog to *Eucyclogobius*. During the late Miocene and Pliocene, much of California was covered with large, occasionally connected, embayments and inland seas that were obliterated by the rapid Plio-Pleistocene uplift of the coastal ranges (Cole and Armentrout, 1979). Intraspecific phylogenetic analyses of *Eucyclogobius* (in progress by Swift and C.B. Crabtree) may help interpret the sequence of these changes.

## CONSERVATION

The disappearance of populations and the vulnerability of those that remain indicate *Eucyclogobius* should be carefully monitored to avoid its complete loss. This is particularly true south of Point Conception where only 15 populations remain: three on Camp Pendleton, one each in the Santa Clara and Ventura rivers, and 10 between Santa Barbara and Point Conception. Today *Eucyclogobius* occurs with a full complement of close relatives (*Clevelandia, Gillichthys, Quietula, Ilypnus*, and *Lepidogobius*) only in Morro Bay, San Luis Obispo County, and Santa Margarita River, San Diego County.

Consideration should be given to restocking lagoons from adjacent populations if habitat conditions seem to have recovered sufficiently to accommodate the species. This means little or no channelization, and allowing lagoons to close off to the ocean for much of the year so that tidal fluctuation is absent or minimal. Fresh unconsolidated sand seems optimal for reproductive burrows and should be available each year. The quality of inflowing water should be kept high. Anecdotal evidence indicates that enrichments from agricultural and sewage effluents cause algal blooms and deoxygenation that restrict the habitable area of lagoons in summer. Little is known of actual tolerances to factors other than salinity. A low-salinity environment (0–15‰) will normally be maintained if the physical integrity of the lagoon remains. Sudden draining of a lagoon in late spring or summer allows marine water to dominate the lagoon for months until winter rains return. Non-native predators should be excluded since circumstantial evidence indicates that they adversely impact *Eucyclogobius*. This applies most to those species tolerant of brackish water such as striped bass, largemouth bass, white catfish, and *Tilapia,* as well as small species such as mosquitofish.

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## APPENDIX

Museum records and locality data (listed north to south) for *Eucyclogobius newberryi:* Localities where fish are apparently rare, but may still occur, are preceded by a +. Sixty-three localities still holding the species in mid-1984 are marked with an asterisk. Distances are straight line (or airline) from point to point as determined from U.S. Geological Survey 7½ minute quadrangle maps.

**Del Norte County.** *(1) Tillas Slough, about 3.2 km SE of mouth of Smith River, LACM 42683-2, about 500 m W mouth Rittmer Creek, seaward of tide gate on Tillas Slough, 19 June 1981; *(2) Lake Earl, 3–6 km N Crescent City, LACM 42669-1, on NE shore at end Buzzini Road, 13 June 1981.

**Humboldt County.** +(3) Freshwater Lagoon, 3–4 km SW Orick on U.S. Hwy. 101, CAS Acc. 1952:x:30, "near shore on highway," 22 August 1951; *(4) Stone Lagoon, 3.5–6.5 km S Orick, LACM 35342-3, vicinity of McDonald Creek on SE shore of lagoon, 31 July 1975; *(5) Big Lagoon, 8.5–13 km S Orick, LACM 35341-1, vicinity of inlet stream and boat ramp (Big Lagoon County Park), 31 July 1975; *(6) Humboldt Bay, LACM 42667-6, NE shore, vicinity oxidation ponds and Radio Station KATA, 13 June 1981, and LACM 35335-5.

**Medocino County.** *(7) Ten Mile River, LACM 35331-1, 0.75 km upstream Hwy. 1 bridge, 29 July 1975; (8) Virgin Creek, about 2 km N Fort Bragg, LACM 35329-2, 28 July 1975; *(9) Pudding Creek, N edge Fort Bragg, LACM 35328-1, 28 July 1975; *(10) Manchester State Beach, 0.75 km N Manchester, two unnamed lagoons, LACM 42666-2, 12 June 1981.

**Sonoma County.** *(11) Salmon Creek, about 1.5 km N Bodega Bay, LACM 35317-3, S shore in Salmon Creek State Beach, 26 July 1975; (12) Cheney Gulch, SE corner Bodega Lagoon, CAS 25512, 12 August 1948; *(13) Estero Americano, 1–1.5 km W Hwy. 1 on Valley Ford–Franklin School Road, LACM 37380-1, 12 October 1977.

**Marin County.** *(14) Estero de San Antonio, crossing of Middle Road, 3.2 km ENE Dillon Beach, LACM 42665-2, 11 June 1981; (15) Walker Creek, near Tomales, USNM 067297, 18 May 1897; +(16) Lagunitas (or Papermill) Creek, CAS (ex UC 263-9-1-A), near Tomales Bay, 18 April 1953; *(17) Rodeo Lagoon, Fort Cronkite, CAS Acc. 1969:vii:16, 17 March 1969; (18) Corte Madera Creek, in Kentfield and Larkspur, CAS 23685, Kentfield

Bridge, 28 October 1961; (19) Novato Creek at Hwy. 101 crossing, 2.5 km SE of Novato, CAS 12995; 19 July 1945.

**Alameda County.** (20) Aquatic Park, west edge of Berkeley, CAS Acc. 1964:xi:13, summer, 1950.

**San Francisco County.** (21) Lake Merced, CAS 12483, 1 November 1895.

**San Mateo County.** *(22) San Gregorio Creek about 16 km S Halfmoon Bay, LACM 35297-2, 22 July 1975; *(23) Pescadero Creek, CAS (uncatalogued), 24 September 1923; *(24) Arroyo de los Frijoles (Bean Hollow), about 6.5 km N Pigeon Point, LACM 35293-2, 21 July 1975.

**Santa Cruz County.** (25) Waddell Creek, about 11.5 km NW Davenport, CAS 28670, 1939–1942; (26) Scott Creek, about 5 km NW Davenport, CAS 20896, 31 August 1939; *(27) Laguna Creek, about 13 km WNW Santa Cruz, LACM 35286-2, 20 July 1975; *(28) Baldwin Creek, about 5.0 km WNW Santa Cruz, LACM 35284-1, 20 July 1975; *(29) Meder Creek, about 0.8 km W Santa Cruz, LACM 35285-2, 20 July 1975; *(30) Moore Creek, Natural Bridges State Beach, N edge Santa Cruz, LACM 43763-1, 3 October 1984; *(31) Twin Lakes (Woods Lagoon) between Santa Cruz and Capitola, LACM 35281-2, eastern lake of two, 19 July 1975; *(32) Rodeo Gulch, Corcoran Lagoon, in Capitola, LACM 35279-1, 19 July 1975; *(33) Aptos Creek, Aptos, LACM 37577-2, 23 July 1977; (34) Pajaro River, CAS 31894, 3 August 1949.

**Monterey County.** *(35) Elkhorn Slough, 250 m W tidegate in Bennett Slough, LACM 42656-2, 8 June 1981; (36) Salinas River, CAS 48290, at Hwy. 1 crossing, 23 August 1951.

**San Luis Obispo County.** +(37) Arroyo del Oso, about 3 km N Piedras Blancas Light, LACM 35257-2, 14 July 1975; *(38) Arroyo del Corral, about 2.2 km N Piedras Blancas Light, LACM 42349-1, 30 June 1981; *(39) Arroyo Laguna (Oak Knoll Creek), 3–4 km N San Simeon, LACM 36195-1, 22 January 1975; *(40) unnamed canyon, 2.2 km NW San Simeon Point, LACM 36663-2, 15 June 1977; (41) Arroyo del Puerto, 0.5 km ESE San Simeon Post Office, LACM 42351-1, 31 January 1981; *(42) Broken Bridge Creek, 1.0 km SE San Simeon Post Office, LACM 42352-1, 31 January 1981; *(43) Little Pico Creek, 2.6 km ESE San Simeon Point, LACM 36666-2, 15 June 1977; *(44) Pico Creek, 3.8 km SE San Simeon Point, SIO 72-88, 14 May 1972; *(45) San Simeon Creek, 6.2 km SE San Simeon Point, SIO 72-87, 13 May 1972; *(46) Leffingwell Creek, 7 km SE San Simeon Point, LACM 42353-1, 31 January 1981; *(47) Santa Rosa Creek, Cambria, LACM 36667-1, 15 June 1977; *(48) Villa Creek, 13.5 km NW Morro Rock, LACM 42355-1, 31 January 1981; *(49) Cayucos Creek, 9.5 km NNW Morro Rock, LACM 36669-1, 15 June 1977; *(50) Old Creek, 7.0 km NNW Morro Rock, LACM 36670-2, 15 June 1977; *(51) Chorro Creek, trib. Morro Bay, LACM 35573-1, 19 January 1976; *(52) Los Osos Creek, trib. Morro Bay, Turri Road, LACM 42348-2, 28 January 1981; (53) San Luis Obispo Creek, 2.3 km ENE Point San Luis, CAS SU 653, 1894; *(54) Pismo (Price) Creek, Pismo Beach, LACM 36673-3, 16 June 1977; *(55) Santa Maria River, 7.2 km N Point Sal, 0.5 km up from Ocean, S shore, LACM 42345-1, 28 January 1981.

**Santa Barbara County.** *(56) Shuman Canyon, 8 km SE Point Sal, LACM 36197-1, 3 November 1976; *(57) San Antonio Creek, 14.5 km SSE Point Sal, LACM 36200-1, 18 July 1975; *(58) Santa Ynez River, S shore, 150 m E railroad tracks, LACM 42343-1, 28 January 1981; *(59) Jalama Creek, 8 km NNW Point Conception, LACM 31425-2, 22 May 1970; *(60) Canada de Cojo, 5.0 km E Point Conception, SBMNH 00956, 27 February 1984; (61) Arroyo St. Augustine, 10.5 km E Point Conception, SBMNH 00015, 25 May 1965; *(62) Canada de las Agujas, 11.7 km E Point Conception, SBMNH 00957, 21 March 1984; *(63) Arroyo Bulito, 10.2 km W Gaviota Creek, LACM 36658-1, 14 June 1977; *(64) Canada de Santa Anita, 7.5–8.0 km W mouth Gaviota Creek, SBMNH 00959, 21 March 1984; *(65) Canada de Alegria, 4.1 km W mouth Gaviota Creek, SBMNH 00961, 21 March 1984; *(66) Canada de Agua Caliente, 2.5 km W mouth Gaviota Creek, LACM 42340-1, 27 January 1981; *(67) Gaviota Creek, Gaviota, LACM 1693, 9 December 1961; (68) Arroyo Hondo, 6.8 km E Gaviota, UMMZ 130666, 23 August 1934; *(69) Arroyo Quemado, about 9.5 km E Gaviota, LACM 36193-1, 27 December 1974; *(70) Tecolote Canyon, about 6.5 km W Goleta, LACM 42339-1, 27 January 1981; *(71) Bell (Ellwood) Canyon, about 6 km W Goleta, SBMNH 1077, 25 September 1984; *(72) Devereaux Slough, 3.2 km W Goleta Point at Coal Oil Point, SBMNH 00592, 1 March 1968; (73) El Estero, Carpinteria, UMMZ 63285, 17 May 1923; (74) Carpinteria Creek, Carpinteria, UMMZ 133067, 8 July 1940.

**Ventura County.** *(75) Ventura River at N edge Ventura, LACM 36216-1, 12 December 1974; *(76) Santa Clara River, between Ventura and Oxnard, LACM 34071-1, 22 September 1974; (77) Calleguas Creek, upper end Mugu Lagoon near Oxnard, UMMZ 133072, 8 June 1940.

**Los Angeles County.** (78) Malibu Creek, 17 km W Santa Monica, UCLA (CAS) W55-272, 12 October 1955.

**Orange County.** (79) Aliso Creek, 0.5 km NW Aliso Point, SW edge Laguna Beach, LACM 42372-1. 7 December 1976; (80) San Juan Creek, 3.3 km E Dana Point, UMMZ 131650, 7 August 1940.

**San Diego County.** (81) San Mateo (San Diego) Creek, N edge Camp Pendleton, LACM 36189-2, 26 December 1974; *(82) San Onofre Creek at San Onofre, LACM 42692-2, 3 December 1981; *(83) Las Flores (Las Pulgas) Creek, about 13 km NW Oceanside, LACM 42691-2, 3 December 1981; *(84) Santa Margarita River, 3.3 km N Oceanside, 5–6 km inland of ocean, LACM 36191-3, 26 December 1974; (85) San Luis Rey River, N edge Oceanside, UCLA W58-1, 10 April 1958; (86) Buena Vista Lagoon, Carlsbad Bird Sanctuary, UCLA 53-235, 10 April 1953; (87) Aqua Hedionda Lagoon, upper (E) end, UMMZ 131809, 29 June 1940.

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# COMPARATIVE FACIAL ANATOMY OF BEAKED WHALES (ZIPHIIDAE) AND A SYSTEMATIC REVISION AMONG THE FAMILIES OF EXTANT ODONTOCETI

JOHN E. HEYNING[1]

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[1] Assistant Curator of Mammals, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

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**ABSTRACT.** The facial regions were dissected on a series of ziphiid, iniid, delphinid, phocoenid, monodontid, and physeterid cetaceans. The distal nasal passages, their diverticula, and adjacent soft anatomy are described for species of the ziphiid genera *Mesoplodon, Ziphius, Hyperoodon, Berardius,* and *Tasmacetus.* Structures found in ziphiids are similar to those found in delphinoid odontocetes and the homologies between them are clear. The junk region of physterids appears to be homologous to the melon of other odontocetes, whereas the spermaceti organ is a neomorph. It was determined that the asymmetry found in the facial soft anatomy and underlying cranium is the primitive condition for all extant odontocetes. This asymmetry is hypothesized to have evolved as a result of selection against dual (bilateral) sound generators that might interfere with each other's signals. A phylogenetic analysis based on anatomical characters provides strong evidence for odontocete relationships that branch off in the following order: Physeteridae, Ziphiidae, Platanistidae, Iniidae, and Delphinoidea.

> "Study of the anatomy of living whales and the bones of extinct species has led to many interesting speculations."
>
> R. Kellogg (1928:29)

## INTRODUCTION

The facial region of cetaceans can be defined as the anatomical region on the dorsal aspect of the skull that includes the nasal passages and the surrounding soft tissues. The nasal passages and surrounding facial structures of odontocete cetaceans form a complex anatomical feature. The nasal passage in this region expands and contracts in width along its length from the bony nares distally to the blowhole and has a series of paired blind-ended diverticula. The surrounding muscles are also complex in their origins and insertions and often interweave, making it difficult to differentiate them from one another. The single external naris and the associated diverticula off the nasal passage are unique to odontocete cetaceans, with no similar structures found in the related mysticete cetaceans (Carte and MacAlister, 1869; Schulte, 1916) that exhibit a more typical mammalian anatomical pattern of simple paired nasal passages.

There are three main areas of zoological interest that can be addressed in a study of this region: (1) an anatomical description and comparision of the facial region among various odontocetes, (2) the use of these anatomical characters for systematics, and (3) questions regarding the function and utilization of this complex morphological region.

The study of odontocete facial anatomy has a long history. The first published description of the facial region was done by John Ray (1671). Numerous anatomical works were published in the late nineteenth and early twentieth centuries. There was then a virtual hiatus in research on odontocete facial anatomy until Lawrence and Schevill (1956) published their classic paper. Later, in the 1960's, the newly formed theory of odontocete echolocation was being advanced. Early on, many researchers implied that the epicranial nasal passage and adjacent structures were the source of certain sounds and hence potentially involved in echolocation (Kellogg, 1961; Lilly, 1961, 1962; Lilly and Miller, 1961; Evans and Prescott, 1962; Norris, 1964). This brought about a renaissance of interest in facial anatomy in the late 1960's and early 1970's. The history of the research on facial anatomy has been reviewed in detail by Mead (1975a). Subsequently, little has been published on either the anatomy or the use of these anatomical characters in systematics. However, a small but important body of literature has arisen since Mead's (1975a) paper that deals directly with the function of the facial structures and is discussed later in this paper.

Facial anatomy has been described in a variety of odontocetes. Most of the work to date has been on the delphinoid families Phocoenidae and Delphinidae, undoubtedly due to availability of specimens from these two groups and to their relatively convenient size for dissection. In the past few decades, a few major works have appeared on the facial anatomy of delphinoid cetaceans (Lawrence and Schevill, 1956; Schenkkan, 1973; Mead, 1975a, and references therein). Recently, Purves and Pilleri (1973), Schenkkan (1973, 1977), Mead (1975a), and Chen et al. (1980) described the facial region in most species of river dolphins (Platanistoidea sensu lato). Description of the facial anatomy of sperm whales (Physeteridae) has focused primarily on the large commercially important species *Physeter catodon* (Pouchet and Beauregard, 1892; Beddard, 1915, 1919, 1923; Raven and Gregory, 1933; Norris and Harvey, 1972; Clarke, 1970, 1978a). However, some work has also been done on the diminutive sperm whales of the genus *Kogia* (Benham, 1901; Kernan and Schulte, 1918; Schenkkan and Purves, 1973). Based on the most widely accepted current taxonomy, there are descriptions in the literature of the facial anatomy of 13 of the 16 genera of delphinids, 3 of 4 genera of phocoenids, both genera of monodontids, both genera of physeterids, all 4 genera of platanistoids, and 2 of the 5 genera of ziphiids. The degree of anatomical detail published obviously varies for each of the above taxa, but clearly the odontocete family of the beaked whales (Ziphiidae) has had the least published on this subject. The only descriptions of this anatomical region are short descriptions of *Mesoplodon bidens* (Schenkkan, 1973), *Hyperoodon ampullatus* (Carlsson, 1888; Kükenthal, 1893; Schenkkan, 1973), and a brief passage regarding *Ziphius cavirostris* by Norris and Harvey (1972). Beaked whales are particularly interesting to look at in this respect because the facial region of skulls from specimens of most species exhibits some degree of sexual dimorphism and extreme cranial asymmetry. Of special interest are the mesorostral ossifications found primarily in adult males of the genera *Mesoplodon* and *Ziphius* (Fraser, 1942; Heyning, 1984) and the resorption of bone anterior to the external bony nares (the prenarial basin) in adult males of *Ziphius*. The first part of this work describes the anatomy of the facial region of several species of ziphiids representing all available genera, discusses the facial region in comparison with other odontocetes, and comments on some functional aspects of the nasal sacs and surrounding structures.

The details of the facial anatomy are also useful as characters in phylogenetic analysis. The beta level taxonomy of cetaceans is poorly known, and the addition of morphological characters is of potential interest. Morphological data sets are valuable especially in cetacean systematics because it is not likely that adequate samples for biochemical data sets will be available in the near future for many rare species. Additionally, only osteological data are directly useful in comparison with extinct taxa. Facial anatomy has been used in the systematics of cetaceans primarily by Mead (1975a) for delphinoid cetaceans. He had some difficulty in using this data set within the Delphinidae because the basic structural plan is consistent at this level and the differences observed are primarily autapomorphies and hence not very useful in higher-level systematics. With this present work describing most of the ziphiid genera, the majority of odontocetes have now been examined and a comprehensive systematic review is now possible. I have used these data in a phylogenetic analysis of the interfamilial relationships among extant odontocetes.

The family Ziphiidae comprises 18 nominal species within five or six genera. Due to their wide distribution, apparent rarity, and often extreme sexual dimorphism, the systematic relationships within this family are imperfectly understood. The genera *Tasmacetus* and *Ziphius* are monotypic. *Berardius* and *Hyperoodon* are usually described as having antitropical species pairs, although many consider *Berardius* to be monotypic (McLachlan et al., 1966; Ross, 1984). The genus *Mesoplodon* is the most species-rich with 12 named species, although Moore (1968) removed the species *M. pacificus* and placed it in the monotypic genus *Indopacetus*. This change has met with mixed acceptance (Mead, 1975a; Rice, 1977; Barnes et al., 1985). I feel that until a full review of the genus *Mesoplodon* is done, it would be premature to remove a single species. The only analysis of relationships among the extant genera of ziphiids was done by Moore (1968) based on cranial features. Mead (1975b) suggested that the fossil genera *Choneziphius, Eboroziphius,* and *Pelycorhamphus* are related to the modern species *Z. cavirostris,* and the fossil genera *Belemnoziphius* and *Proroziphius* are related to the extant genera *Mesoplodon* and *Hyperoodon.*

## FACIAL ANATOMY OF ZIPHIIDS

### MATERIALS AND METHODS

Dissections were done on a series of heads from various ziphiid species. Different dissecting techniques were used among specimens in order to better understand the spatial relationships between various structures; these included superficial to deep dissections as well as transverse and longitudinal sectioning of the soft tissues at various positions. Due to the rarity of ziphiid specimens, I was not able to serial-section the entire head, which would damage the skull, as has been done by other workers on delphinids (Hosokawa and Kamiya, 1965; Mead, 1975a).

Numerous heads from specimens representing other odontocete families were also dissected for comparative purposes. This is important because many of the discussions in previous anatomical works are based on interpretations regarding a structure's function or its homolog in another species. For example, Norris et al. (1971) hypothesized a scenario of air recycling through a passage that is in fact a blind-ended sac (accessory sac), based on a misinterpretation of Lawrence and Schevill's (1956) description and nomenclature of this sac (connecting sac). In order to best evaluate structures in terms of homology, it is necessary to dissect them rather than rely on subjective interpretations drawn from the literature. Fetuses were also dissected to help establish homologies and determine the polarity of certain characters. I was unable to secure any specimens of *Platanista* spp. and must depend on published accounts for the family Platanistidae (sensu stricto). Photographs, drawings, measurements, and notes were taken at each dissection.

The specimens used in this study are listed in Table 1. For the specimens that have not been catalogued into collections at this time, I provide the field numbers and the acronyms of the institutions in which they are placed. I was not able to secure specimens of the ziphiid genera *Hyperoodon* and *Tasmacetus* for dissection. However, *Hyperoodon ampullatus* has been briefly described in the literature, and James Mead of the Smithsonian Institution kindly provided me with his unpublished notes from his dissection of an adult female specimen of *Tasmacetus shepherdi.*

### TERMINOLOGY

In order to discuss the anatomy of the facial region of ziphiids clearly, I shall first define the terminology used in this work. Because soft tissues of the facial region are usually described with reference to the skull, I shall rely on it for landmarks (Figs. 1, 2). Kernan (1918) provided an excellent detailed description of the skull of *Ziphius cavirostris,* and his terminology will be used preferentially. I have tried to avoid, as much as possible, the creation of new terms. The terminology used also applies

Table 1. List of specimens dissected in this study. Institutional acronyms are: HSUZ, California State University at Humbolt; LACM, Natural History Museum of Los Angeles County; NMML, National Marine Mammal Laboratory; OSU, Oregon State University; PSU, Portland State University; SBMNH, Santa Barbara Museum of Natural History; T A&M, Texas A&M University; USNM, National Museum of Natural History.

| Species | Sex | Length (cm) | Institution | Number |
|---|---|---|---|---|
| Ziphiidae | | | | |
| *Ziphius cavirostris* | M | 555 | HSUZ | 4471 |
| *Ziphius cavirostris* | F | 064 | LACM | 84082 |
| *Ziphius cavirostris* | M | 491 | T A&M | C-172 |
| *Ziphius cavirostris* | M | 447 | USNM | 550803 |
| *Ziphius cavirostris* | M | 256 | USNM | 550735 |
| *Ziphius cavirostris* | F | 512 | USNM | 550734 |
| *Ziphius cavirostris* | M | 265 | PSU | 86-11 |
| *Mesoplodon bidens* | M | 457 | USNM | 550414 |
| *Mesoplodon carlhubbsi* | M | 248 | LACM | 84043 |
| *Mesoplodon carlhubbsi* | F | 256 | LACM | 84018 |
| *Mesoplodon carlhubbsi* | M | 404 | SBMNH | 3139 |
| *Mesoplodon carlhubbsi* | M | 297 | HSUZ | VM 832 |
| *Mesoplodon carlhubbsi* | M | 480 | HSUZ | VM 851 |
| *Mesoplodon stejnegeri* | M | 525 | OSU | — |
| *Mesoplodon stejnegeri* | F | 237 | LACM | 84066 |
| *Mesoplodon densirostris* | F | 410 | USNM | 550338 |
| *Mesoplodon densirostris* | F | 433 | SBMNH | 3138 |
| *Mesoplodon densirostris* | M | 420 | USNM | 550754 |
| *Mesoplodon densirostris* | F | 397 | USNM | 550746 |
| *Berardius bairdii* | M | 790 | USNM | 550895 |
| *Berardius bairdii* | F | 183 | USNM | 550890 |
| Physeteridae | | | | |
| *Physeter catodon* | M | 440 | LACM | 72545 |
| *Physeter catodon* | ? | 074 | LACM | 27066 |
| *Physeter catodon* | ? | 025 | LACM | 72155 |
| *Kogia breviceps* | M | 279 | LACM | 84044 |
| *Kogia simus* | M | 168 | LACM | 72533 |
| *Kogia simus* | M | 224 | USNM | 550487 |
| Phocoenidae | | | | |
| *Phocoena phocoena* | M | 114 | LACM | 72338 |
| *Phocoena phocoena* | F | 138 | LACM | 72563 |
| *Phocoena phocoena* | M | 134 | LACM | 84016 |
| *Phocoenoides dalli* | M | 213 | LACM | 84048 |
| *Phocoenoides dalli* | M | 198 | LACM | 84017 |
| *Phocoenoides dalli* | F | 194 | NMML | MWL 136 |
| Delphinidae | | | | |
| *Delphinus delphis* | M | 209 | LACM | 84071 |
| *Delphinus delphis* | F | 193 | LACM | 84083 |
| *Cephalorhynchus commersoni* | F | 150 | USNM | CC-8329 |
| *Cephalorhynchus commersoni* | F | 144 | LACM | 84013 |
| *Grampus griseus* | M | 140 | LACM | 84022 |
| *Lagenorhynchus obliquidens* | M | 235 | LACM | 84023 |
| *Lagenorhynchus obliquidens* | M | 179 | LACM | 84014 |
| *Lagenorhynchus obliquidens* | F | 223 | LACM | 84063 |
| *Lissodelphis borealis* | F | 223 | LACM | 72573 |
| *Orcinus orca* | F | 245 | LACM | 72453 |
| *Orcinus orca* | F | 240 | LACM | 72577 |
| *Pseudorca crassidens* | M | 480 | LACM | 84047 |
| *Tursiops truncatus* | M | ? | LACM | 84010 |
| *Tursiops truncatus* | ? | ? | LACM | 84070 |
| Monodontidae | | | | |
| *Delphinapterus leucas* | F | 266 | LACM | 84081 |
| Iniidae | | | | |
| *Inia geoffrensis* | ? | ? | USNM | 571263 |
| *Pontoporia blainvillei* | ? | ? | USNM | — |

broadly to most odontocetes. For each term listed below, I have listed in parentheses synonymies and the author who first coined the term if known. Terms defining structures of facial soft anatomy are italicized and discussed in the next section on the generalized delphinid.

*Facial border* (new term). This border is defined as the ridge formed on both sides by the contact of the lateral and posterior edges of the maxillae with the supraorbital processes of the frontals and supraoccipital. Thus, this ridge extends on either side, from the antorbital region posteriorly, and then medially, to the vertex of the skull. The facial border defines the lateral and posterior boundaries of the facial region of the skull. Kernan (1918:352) referred to the occipital region of this border as the transverse crest.

*Facial fossa* (Kernan, 1918). This is the surface of the maxillae that lies between the facial border laterally and posteriorly, and the premaxillae medially. This surface is weakly to strongly concave in ziphiids. The facial fossa is the site of origin of the major nasofacial muscles.

*Vertex* (Flower, 1872; = synvertex, Moore, 1968). This is the elevated region of the skull immediately posterior to the bony nares that consists of the most dorsal sections of the nasals, maxillae, and premaxillae. The term vertex has been used for other odontocetes quite frequently although the vertex is not as pronounced as it is in ziphiids (Figs. 1, 2). Therefore, to be consistent with the majority of published works, I shall use this term rather than Moore's term "synvertex" that refers to the same feature, but only in ziphiids.

*Prenarial basin* (= pre-nasal fossa, Turner, 1872; = prenarial fossa, Owen, 1870). This is the region of secondary resorption of bone anterior to the external bony nares that appears with presumably advancing age in male *Ziphius cavirostris* (Fraser, 1942). The prenarial basin is also found in the fossil ziphiid genera *Pelycorhampus, Choneziphius, Ziphirostrum, Eboroziphius* (Mead, 1975b), and *Proroziphius*. The bones affected by this resorption include the premaxillae, maxillae, and the vomer.

*Mesorostral canal* (= mesorostral furrow, Turner, 1880; = supervomerine canal, Mead, 1975b). This is the longitudinally oriented gutter anterior to the nares that is bordered laterally by the premaxillae and ventrally by the vomer. It is found in all cetaceans and is filled with hyaline cartilage in life. The term mesirostral often has been used in the literature, but the term mesorostral (Flower, 1878) has priority I believe.

*Mesorostral ossification* (= mesorostral bone, Turner, 1872). This is the secondary dorsal intrusion of dense bone from the vomer and to a lesser extent from the premaxillae that fills, with age, the mesorostral canal. This deposition of bone is usually found only in adult males of the genera *Mesoplodon, Ziphius,* and to a lesser extent *Berardius* (Heyning, 1984).

*Maxillary ridge* (True, 1910; = maxillary tuberosity, Flower, 1872; = maxillary prominence, Moore and Wood, 1957). This ridge on each maxilla is oriented longitudinally along the lateral side of the facial fossa. The vertical elevation of this ridge varies among species of ziphiids. In some species, the ridge terminates anteriorly onto the antorbital tubercle, whereas in others it terminates onto the maxillary tubercle, and in *Hyperoodon* spp. it terminates on the rostrum medial to the antorbital notch. In *Hyperoodon* spp., these ridges are extremely elevated and are generally referred to as maxillary crests. The term maxillary crests was originally used to define the large dorsally oriented flanges of the maxillae in *Platanista* spp. (Anderson, 1878) and Barnes (1985*a*) used this term to define the lower ridges found on the skulls of pontoporiids (sensu Barnes, 1985*a*). I will use the term maxillary ridge for any such feature that is low to moderate in elevation and restrict the term maxillary crest for the extreme development of this structure in *Hyperoodon* spp. and *Platanista* spp.

*Supraorbital process.* This is the lateral flange of bone that covers the orbit dorsally. Its ventral surface is formed by the frontal and its dorsal surface consists primarily of the maxilla. It is found on the skulls of all cetaceans. The maxillary ridge, when present, is situated on the dorsal surface of the supraorbital process.

*Antorbital notch.* This notch is visible in dorsal and ventral views at the posterolateral ends of the rostrum. It is rather pronounced in most species of odontocetes. The facial nerve exits the cranium in the orbital region and sweeps dorsally within this notch to innervate the facial muscles. In *Mesoplodon carlhubbsi,* there is a pair of notches on both sides of the antorbital region. Moore (1963) coined the term prominential notch (Fig. 8) for the more medial notch.

*Antorbital tubercle.* This anteriorly directed process forms the lateral surface of the antorbital notch. It is formed by contributions from both the maxilla and lacrimal. In *Mesoplodon carlhubbsi,* the small accessory process medial to the antorbital tubercle was termed the maxillary prominence (Fig. 8) by Moore (1963).

*Spiracular plate* (Moore, 1963; = premaxillary sac fossa, Fordyce, 1981). This feature is formed by the laterally expanded dorsal surface of the premaxillae lateral and anterior to the bony nares. The premaxillary sacs are found adjacent to this surface. The spiracular plate is absent in physeterids. In the same publication, Moore (1963) used the term prespiracular plate for the same feature.

*Spiracular surface of vertex* (new term). This is the anterior surface of the vertex of ziphiids that extends from the bony nares dorsally to the top of the vertex and laterally to the edge of the premaxillae. It is along this surface that the posterior nasal sacs are situated.

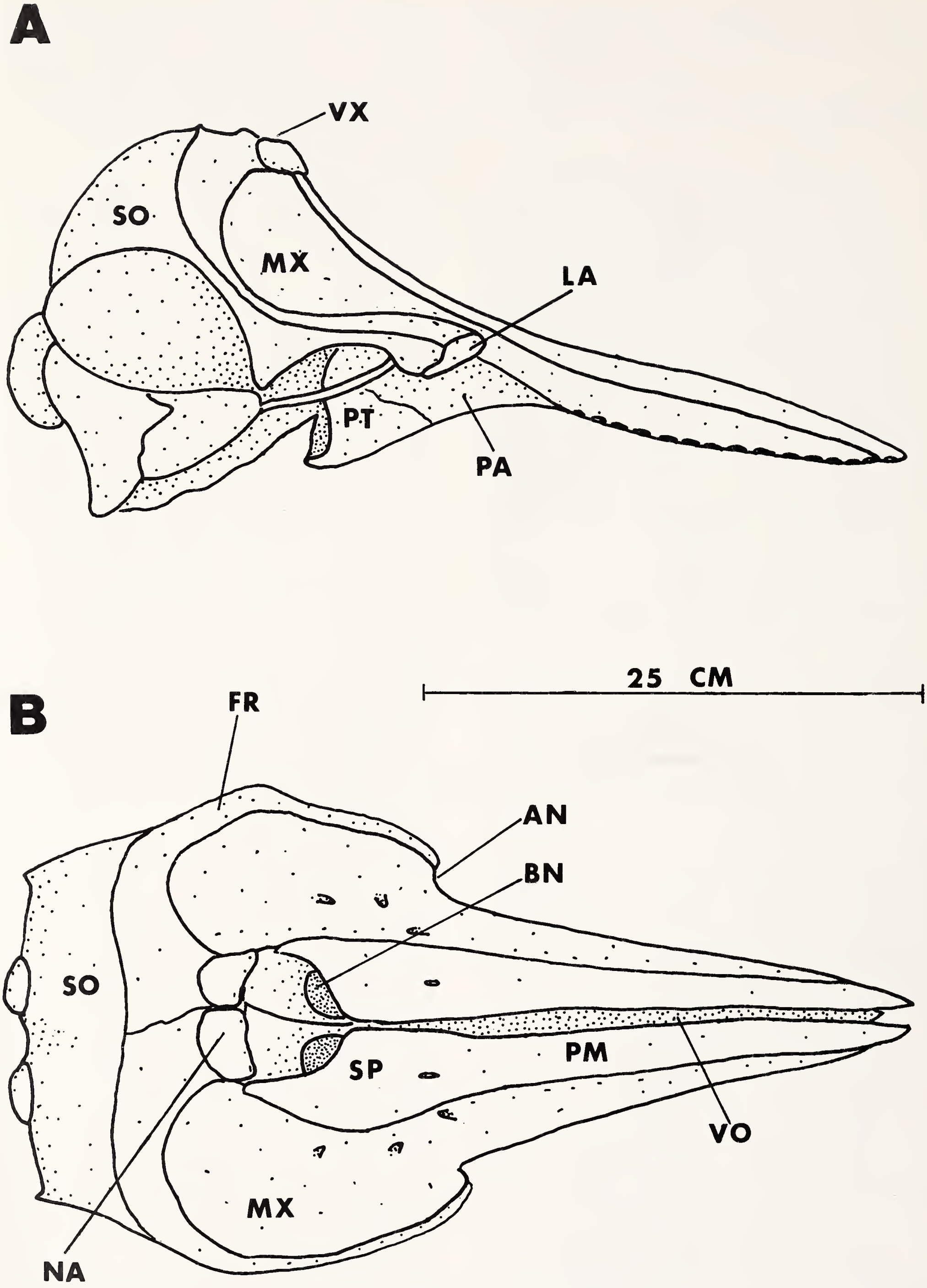


**Figure 1.** **A,** Lateral view; **B,** dorsal view of the skull of a typical delphinid *Tursiops truncatus,* note the gradually sloping profile of the facial region and the relatively low vertex. AN = antorbital notch, BN = bony naris, LA = lacrimal, MX = maxilla, NA = nasal, PA = palatine, PM = premaxilla, PT = pterygoid, SO = supraoccipital, SP = spiracular plate of premaxilla, VO = vomer, VX = vertex.

## GENERALIZED DELPHINID

A brief description of a generalized delphinid will be presented first because most previous studies have centered on species within this family. The following is based on the descriptions by Lawrence and Schevill (1956), Schenkkan (1973), and Mead (1975a). This generalized model (Fig. 3) is used in comparison with the anatomy of various ziphiids.

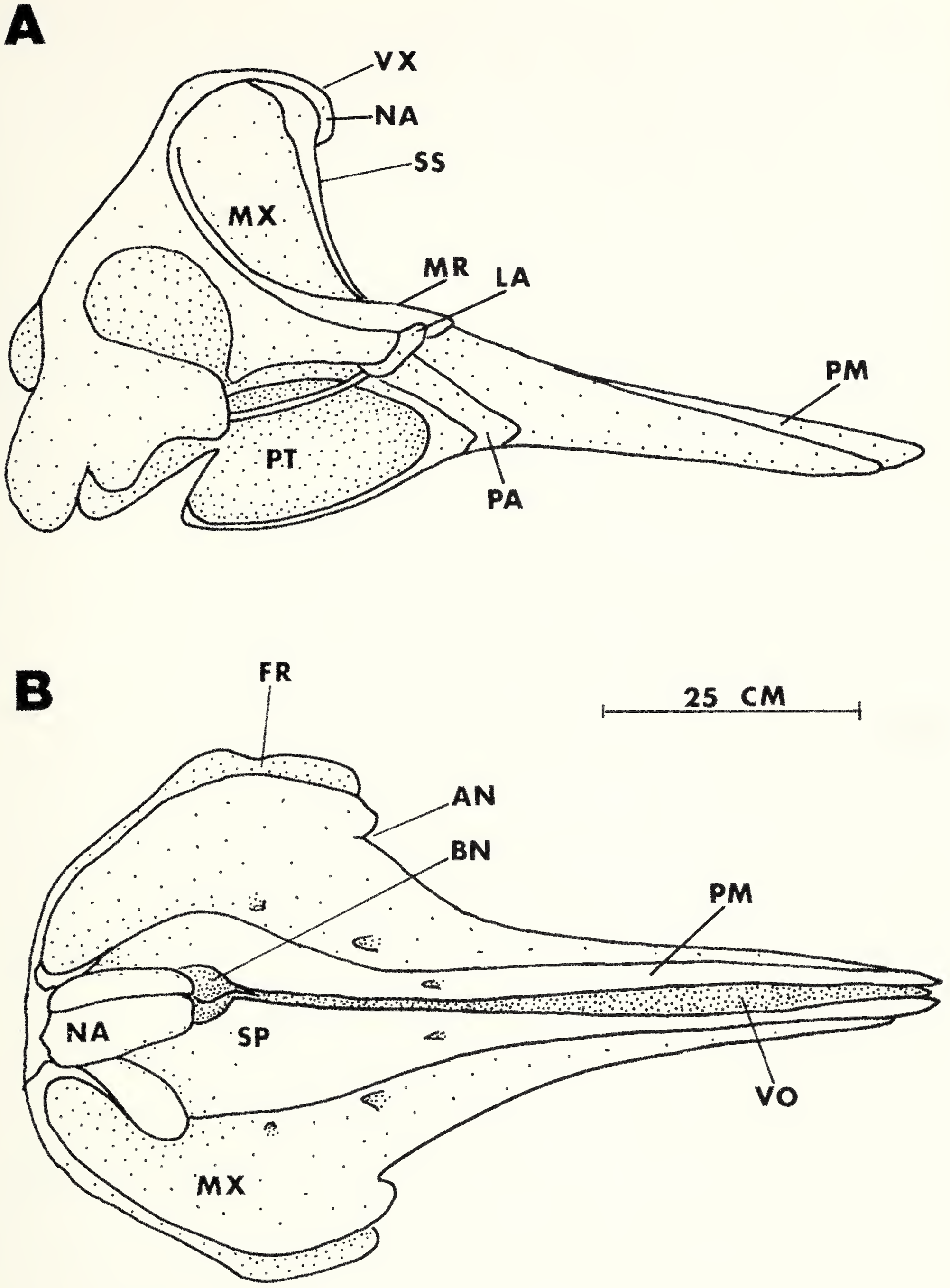


Figure 2. A, Lateral view; B, dorsal view of the skull of the ziphiid *Ziphius cavirostris,* note the elevated vertex. AN = antorbital notch, BN = bony naris, LA = lacrimal, MR = maxillary ridge, MX = maxilla, NA = nasal, PA = palatine, PM = premaxilla, PT = pterygoid, SP = spiracular plate of premaxilla, SS = spiracular surface of vertex; VO = vomer, VX = vertex.

Following the species descriptions of beaked whales, I have then summarized the morphological features of each odontocete family for comparison.

The section on each species begins with a description of the nasal passages and sacs, beginning superficially and proceeding to deeper structures. Following this, the surrounding soft anatomy, including the muscles, is described in the same order. For continuity, Mead's (1975a) terminology is used when applicable. Previous anatomical synonyms in the literature were reviewed by Mead (1975a) and readers should refer to that work.

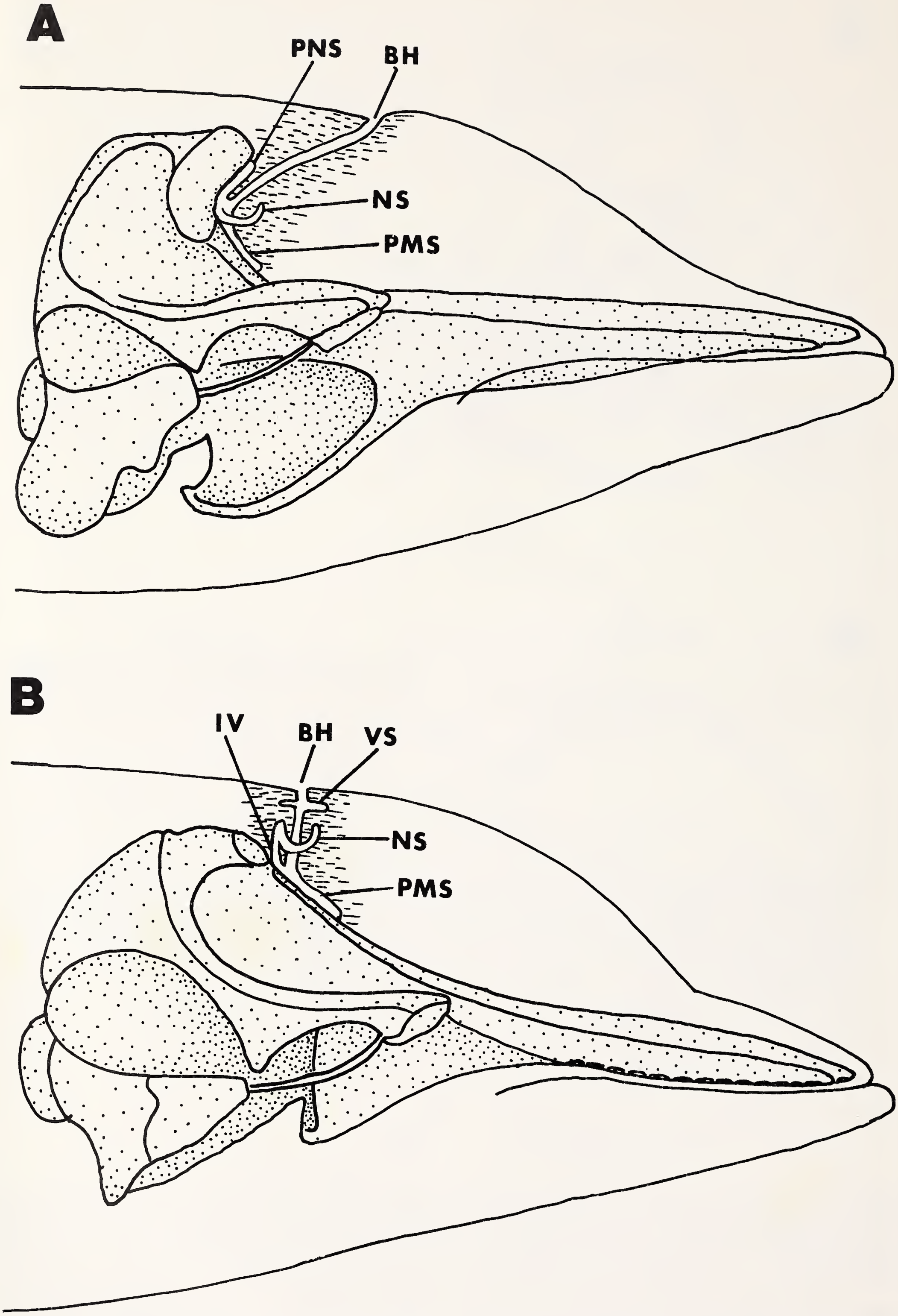


**Figure 3.** Lateral diagrammatic view of the nasal passages and diverticula of **A,** *Mesoplodon carlhubbsi* and **B,** *Tursiops truncatus.* BH = blowhole, IV = inferior vestibule, NS = nasofrontal sac, PMS = premaxillary sac, PNS = posterior nasal sac. Illustrations are not to scale.

### Nasal Passages

The external naris or *blowhole* is a shallow to moderately deep lunate slit with anteriorly directed apices. The single nasal passage or *vestibule* extends in a vertical plane to the bony nares. A series of blind sacs or diverticula branch off the nasal passage.

The most superficial one is the large *vestibular sac* that is typically located a few cm below the surface of the head. It is a broad flat distensible sac that lies in a plane approximately parallel to that of the external surface of the head. Its shape varies from species to species, but it usually extends laterally, posteriorly, and slightly anteriorly from the nasal passage. The vestibular sacs among species of delphinids vary in the degree of division into two bilaterally paired diverticula.

Originating from the posterolateral aspect of the nasal passage at a deeper level are a series of paired diverticula. The most lateral are the small tubular sacs that extend laterally and anteriorly and are termed the *accessory sacs.* Originating medial and posterior to this are the *inferior vestibules* that are also often tubular in cross section and extend dorsally posterior to the nasal passage. They terminate dorsally as the horizontally oriented horseshoe-shaped *nasofrontal sacs.* The posterior curves of these nasofrontal sacs extend medially posterior to the nasal passage and the anterior sections of these sacs extend anterior to the nasal passage within the tissue of the nasal plug (see Soft Anatomy).

Anteriorly, at the junction of the nasal passage and the bony nares are the paired *premaxillary sacs.* These broad flat ovoid sacs lie along the spiracular surfaces of the premaxillae and open to the nasal passages at their posterior border. The premaxillary sacs are the largest diverticula in most delphinids.

### Soft Anatomy

There are two layers of very thin and highly variable superficial muscles in delphinids. Most superficial is the *pars posteroexternus* that originates from the supraorbital process and sweeps dorsally to the vertex and the connective tissue surrounding the blowhole. Deep to this muscle is the *pars intermedius* that has a similar origin just medial to the pars posteroexternus but with fibers that extend over the facial region farther anteriorly to insert into the connective tissue of the melon. Both of these muscles may be absent in some species and are even variable in presence within a species. Both of these muscles also have portions that pass dorsal to the vestibular sac. The next deeper muscle, the *pars anteroexternus,* is larger and not variable in its presence. It is a moderately thin muscle that originates broadly from the entire facial border. Its fibers converge toward, and insert onto, the connective tissue surrounding the distal nasal passage and vestibular sac. The *pars posterointernus* is a thicker muscle that originates from the posterior aspect of the facial fossa with converging fibers that insert onto the medial connective tissue posterior to the nasal passage and dorsal to the posterior aspect of the nasofrontal sac. The last and deepest major facial muscle is the *pars anterointernus.* It is by far the largest facial muscle by mass and originates in most of the facial fossa deep to all the other facial muscles. The posterior fibers of this muscle run anteriorly to insert on the connective tissue anterior to the anterior aspect of the nasofrontal sac. More anterior fibers are oriented more medially and pass dorsally to insert into the melon. The most anterior fibers of this muscle originate anteriorly along the rostrum and are termed the *rostral muscles.* These muscles usually can be subdivided into a lateral rostral muscle and a medial rostral muscle.

There is a small complex group of muscle fibers that surround the nasofrontal sac termed the *intrinsic muscle.* The nasofrontal sacs are the only diverticula in delphinids with a small intrinsic muscle. Another small muscle, the *diagonal membrane muscle,* originates from the dorsolateral aspect of the vertex and has fibers that are oriented anteroventrally to insert on the margins of the paired diagonal membranes within the bony nares.

Occluding the bony nares are a pair of large fleshy lobes of tissue called the *nasal plugs* (see Fig. 24); these consist primarily of connective tissue and fat. They form the dorsal surfaces of the premaxillary sacs and have well-defined lateral edges termed the lateral lips. The anterior section of the nasofrontal sacs extends medially into these plugs. The nasal plugs are retracted by paired *nasal plug muscles* that originate from the premaxillae anterior and lateral to the premaxillary sacs.

Farther anterior on the facial region is a large ovoid *melon,* which is a region of adipose tissue with a varying amount of connective tissue within in. The melon typically is set asymmetrically, slightly off to the right side. The melon has a core region of fatty tissue with little connective tissue in it. This "inner melon" core has a higher lipid content and a different lipid composition than the surrounding outer melon and blubber (Litchfield et al., 1973; Norris and Harvey, 1974). The melon core typically extends posteriorly into the right nasal plug but extends only slightly, if at all, into the left nasal plug.

The *blowhole ligament* is a band of dense connective tissue fibers that originates from the premaxillae and extends around behind the nasal passage near the vertex of the skull. The apertures of the accessory sacs and the inferior vestibules are behind this ligament, and the sacs extend laterad and dorsad to this ligament, respectively (see Mead, 1975a; Fig. 4).

## FAMILY ZIPHIIDAE

The description of ziphiid facial anatomy begins with detailed accounts of species of *Mesoplodon* because I had more specimens of this genus avail-

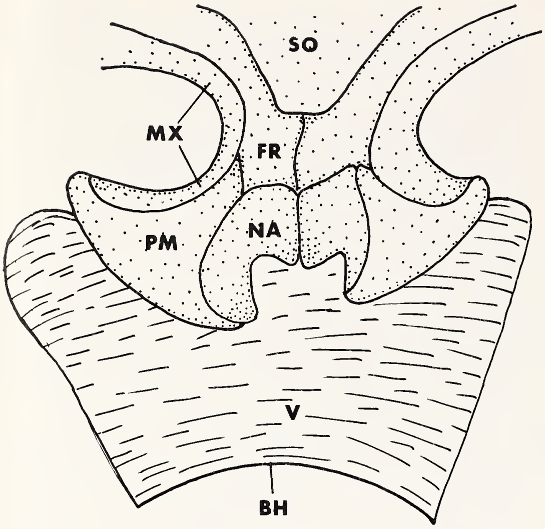


**Figure 4.** Diagrammatic dorsal view of the nasal vestibule of *Mesoplodon carlhubbsi* from the blowhole posterior to the vertex of the skill. BH = blowhole, FR = frontal, MX = maxilla, NA = nasal, PM = premaxilla, SO = supraoccipital, V = vestibule.

able and therefore can comment somewhat on the extent of individual, sexual, and ontogenetic variation in the facial anatomy. This does not imply that the genus *Mesoplodon* is typical or primitive among the ziphiids or that it provides a generalized plan. In fact, it is one of the most derived groups in most features of its cranial anatomy. The genera *Berardius* and *Tasmacetus* seem to be most primitive in regard to development of the vertex and reduction of the dental formula among modern ziphiids (Moore, 1968).

### *Mesoplodon carlhubbsi*

**Nasal Passages.** The nasal passages become confluent in *Mesoplodon carlhubbsi* immediately distal to the bony nares. This pattern is found in all ziphiids, delphinoids, iniids, and platanistids. The nasal passage continues as a single tube and opens superficially as a single blowhole (Fig. 3).

The blowhole is a shallow transverse lunate slit with apices directed forward (Fig. 4). The entire blowhole is set slightly off to the left side and the right margin is slightly anterior to the left. The blowhole is situated approximately 5 cm anterior to the vertex of the skull. The vestibule of the naris is a wide dorsoventrally flattened tube when relaxed and is oriented in a posteroventral plane of about 45° from the horizontal. It enlarges laterally as it approaches the spiracular surface of the vertex (Fig. 4), where it extends laterally beyond the bone approximately 1 cm on the left side and 2 cm on the right. The vestibule is asymmetrical in that it is relatively larger on the right side. Correspondingly, the underlying right nasal plug is approximately twice the width of the left nasal plug. The vestibule in this species, as in all odontocetes examined, was lined with a black squamous epithelium; this agrees with the observations of Mead (1975a). There is no evidence of a vestibular sac (Fig. 3) as has been described in delphinoids and iniids.

There are a series of diverticula that lie posterior and lateral to the nasal passage along the spiracular surface of the skull (Figs. 3, 5). The aperture to these diverticula opens from beneath the blowhole ligaments. The leading edge of the blowhole ligament is tightly drawn against the spiracular surface of the vertex, but the nasal sac dorsal to it has loose distensible walls and folds over anterior to the ligament. This makes for a highly distensible sac with a tight, flat, and broad aperture. This sac is appressed to the lateral spiracular surface and connects laterally with the anterior section of the nasofrontal sac and the diminutive outpocket termed the accessory sac (Figs. 3, 5). These sacs are separated from the premaxillae apparently only by epithelium and periosteum. This also appears to be the case for the premaxillary sacs of delphinids (Mead, 1975a). These posterior sacs adjacent to the spiracular surface of the vertex are homologous with both the inferior vestibule and posterior nasal sacs of phocoenids, monodontids, platanistids, and iniids. For simplicity, I will term these sacs the posterior nasal sacs, realizing that the ventral portions are homologous to the inferior vestibules of delphinids, etc. The sizes of the posterior nasal sacs are approximately equal to the size of the spiracular surface. The spiracular surface is larger on the right side, and thus the right posterior nasal sac is larger than the left.

The paired anterior sections of the nasofrontal sacs (Figs. 3, 5) extend laterally at approximately the midlevel of the bony nares. The right sac curves sharply anteriorly and extends in a horizontal plane medially into the right nasal plug to approximately the midline of the facial region. The left nasofrontal sac extends anteriorly and medially approximately 1 or 2 cm. These anterior segments of the nasofrontal sacs average 0.5 cm in diameter. There are small (< 1 cm) and wide blind outpockets that appear to be the accessory sacs; these are only slightly ventral and anterior to the apertures of the nasofrontal sacs.

The paired premaxillary sacs are situated adjacent to the spiracular plate of the premaxillae. They are roughly rectangular with bluntly rounded corners. The apertures of these sacs to the nasal passage are located along the lateral and anterior aspect of the bony nares. These sacs are asymmetrical, with the right sac extending further laterally and slightly more anteriorly than the left sac. They are flattened dorsoventrally, with the nasal plugs forming the dorsal surfaces. The right and left sacs are separated by a medial fold of connective tissue that originates from the mesethmoid and extends dorsally into, and through, the nasal plugs. In general appearance, these sacs are similar to the premaxillary sacs of delphinoids, iniids, and platanistids.

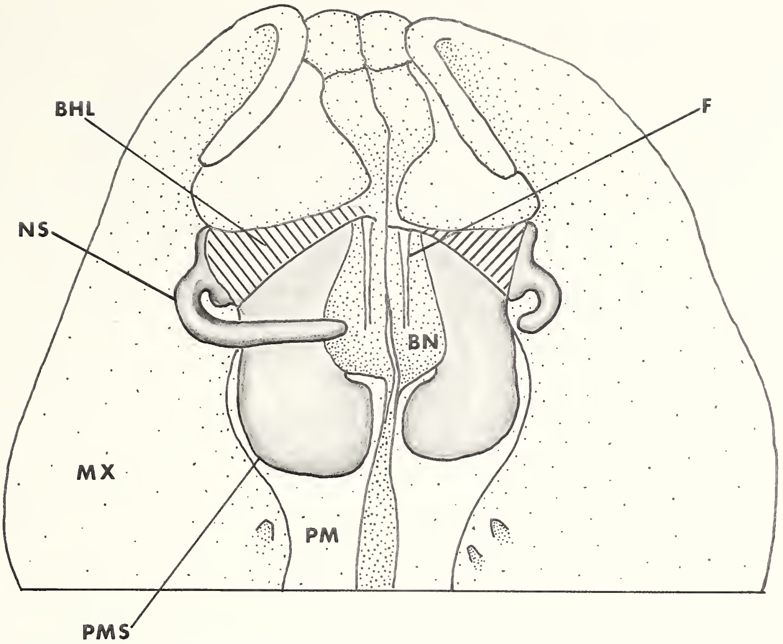


**Figure 5.** Anterodorsal view of the nasal diverticula of *Mesoplodon carlhubbsi.* The hatched region represents the blowhole ligaments behind which lie the paired posterior nasal sacs. Note fold of tissue on posterior wall of the bony naris. These folds may be homologous to the diagonal membrane of delphinids. BHL = blowhole ligament, BN = bony naris, F = fold of tissue, MX = maxilla, NS = anterior section of nasofrontal sac, PM = premaxilla, PMS = premaxillary sac.

**Soft Anatomy.** Posteriorly on the head, the hypodermis or blubber is quite distinct from the underlying superficial fascia to approximately the level of the eye. Anterior to this, the connective tissue of the blubber grades continuously into the connective tissue of the melon deep to it. Under the skin and blubber, the anterior exposed surface of the melon is composed of very loose connective tissue fibers within dense areolar tissue (Fig. 6). Closer to the blowhole and at the antorbital region, there are very distinct regions of dense connective tissue fibers with little adipose tissue in them. In the region of the facial fossa, there are several layers of fascia superficial to the facial muscles. The external fascial layer passes dorsally as a thin band from the supraorbital process just posterior to the eye straight

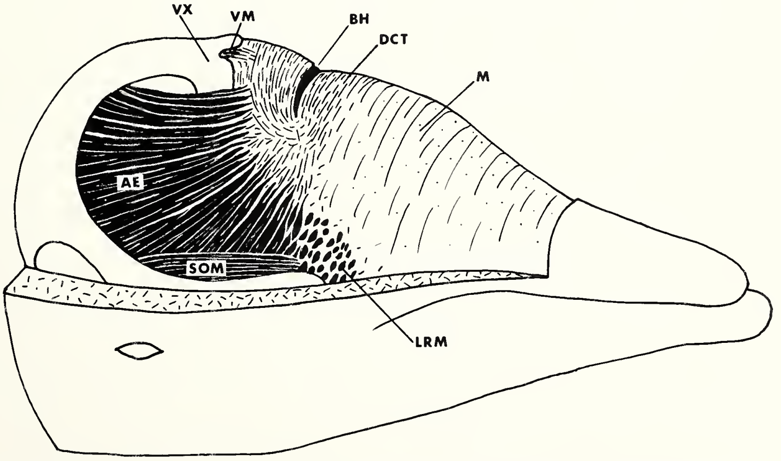


**Figure 6.** Diagrammatic dorsolateral view of the facial anatomy of *Mesoplodon carlhubbsi* with the blubber layer and superficial fascia removed. The most posterior insertion of the lateral rostral muscle onto the blubber layer (removed) can be clearly seen here. AE = pars anteroexternus muscle, BH = blowhole, DCT = dense connective tissue, LRM = lateral rostral muscle, M = melon, SOM = supraorbital muscle, VM = muscle of vertex, VX = vertex.

upward to the vertex. In the next layer underneath this are fibers that run anterodorsally toward the blowhole region but become very diffuse in the region of the blowhole. Also coming from the antorbital process are fibers that run at right angles to the preceding layer and sweep upward posteriorly to become continuous with the dense connective tissue around the nasal passage.

The thin and highly variable superficial muscles found in delphinids (Mead, 1975a), the pars posteroexternus and the pars intermedius, were not evident in any *Mesoplodon* specimen I dissected.

The pars anteroexternus is large and distinct (Fig. 6). This broad yet thin muscle originates along the facial border (Fig. 8) and inserts onto the broad thick aponeurotic sheet surrounding the blowhole. Thus, the paired pars anteroexternus muscles on either side of the vertex converge medially and anteriorly. I was able to separate the pars anteroexternus clearly from the deeper muscles along the vertex as far forward as the supraorbital region, but this muscle becomes diffuse and weakly defined anteriorly. This muscle averages 0.5–1.0 cm in thickness. The pars anteroexternus of all *Mesoplodon* spp. dissected extends over the lateral edges of the premaxillae on the vertex.

On the vertex of the skull is a thin mass of connective tissue and muscle that is difficult to differentiate laterally from the pars anteroexternus muscle. However there appears to be a small distinct muscle of the vertex itself with fibers oriented longitudinally (Fig. 6). I have defined this as the vertex muscle. It originates primarily from the anterior and dorsal surfaces of the nasals but takes some of its origin from the premaxillae and inserts on the connective tissue mass on the dorsal aspect of the vestibule posterior to the blowholes. I noted this muscle only in young specimens of *Mesoplodon carlhubbsi* and did not find it in any other specimens.

There is a region of very dense connective tissue on the anterior maxillary ridge, lateral to the blowhole. This dense mass is in the anatomical region of the maxillary crests of *Hyperoodon* spp. and may be analogous to it. There is a small thick muscle that originates from the lateral aspect of the supraorbital process and inserts onto the lateral edge of this dense connective tissue mass (Fig. 6). This muscle, here termed the supraorbital muscle, is quite distinct from the pars anteroexternus that passes deep to it. Schenkkan (1973) appears to have illustrated this muscle in *Mesoplodon bidens* in his figure 6, but did not label it or discuss it in the text. Mead (1975a:fig. 10) labeled this muscle in the delphinid *Stenella plagiodon* (= *S. frontalis*) as the rostral muscle. Because this muscle has fibers that are oriented along the longitudinal axis of the skull, and because the true rostral muscles have fibers that originate from the rostrum and spread dorsally and laterally, I believe these two muscles are distinct.

Deep to the pars anteroexternus is the much larger pars anterointernus muscle whose fibers originate broadly from the entire facial fossa (Figs. 7, 8). The pars anterointernus is fairly symmetrical. The most posterior fibers of the two sides meet and interweave on the anterior surface of the spiracular surface of the vertex. The more anterior fibers of this muscle are more complicated, with origins along the medial aspect of the rostrum and insertions on the ventrolateral aspect of the connective tissue of the nasal passage. Because the insertions of the anterior and posterior fibers differ in this way, the posterior portion is slightly folded over the more posterior of the fibers that insert upon the nasal passage (Fig. 7). The internal architecture of this muscle is quite complex. It consists of thin sheets of muscle imperfectly separated by thin fascial planes. This laminated muscle is often folded over itself, especially in the posterior region of the facial fossa. This feature is characteristic of all ziphiids and delphinoids I have dissected and is clearly illustrated in the delphinid *Stenella plagiodon* (= *S. frontalis*) by Mead (1975a:fig. 10).

At the vertex, there is a fascial plane where it is relatively easy to separate both the pars anteroexternus and the pars anterointernus. On the supraorbital process, the lateral ridge, which terminates anteriorly as the antorbital tubercle, is the site of origin for the pars anteroexternus, and the more medial maxillary ridge, which ends as the maxillary prominence, is the site of lateral origin of the pars anterointernus, at least in *Mesoplodon carlhubbsi* (Fig. 8) that has both ridges well developed (Moore, 1963). The separation of these two muscles is slightly visible in transverse section at the antorbital region. The majority of the dorsal thick and dense connective tissue connects to the pars anteroexternus. There is no evidence of the distinct pars posterointernus described in delphinids by Mead (1975a).

The well-defined rostral muscles originate along the lateral aspect of the rostrum and radiate laterally and dorsally. There are two of these muscles, which agrees with Mead's (1975a) description of a lateral and a medial rostral muscle. The lateral muscle is much larger anteriorly. It has fibers several cm long, and the muscle itself is approximately 3 cm thick.

In a transverse section at about mid-rostrum, the lateral rostral muscle appears to be slightly larger on the left side. On the right side, the adipose tissue of the asymmetrically situated melon takes up some of the space occupied by this muscle on the left side. The fibers of the small medial rostral muscle appear to be oriented anteroposteriorly as evidenced by a sagittal section. Further posteriorly, a transverse section at the level of the antorbital notches is approximately at the anterior edge of the blowhole. In this region it can be seen distinctly that the lateral rostral muscle originates on the lateral aspect of the maxillae and that the medial rostral muscle originates primarily on the dorsal surface of the premaxillae and inserts on the ventrolateral aspect of the melon. The much larger lateral muscle inserts on the lateral and ventral surfaces of the

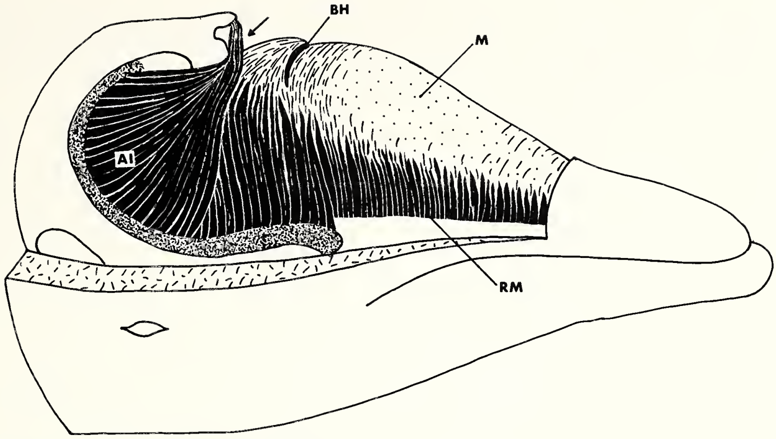


**Figure 7.** Diagrammatic dorsolateral view of *Mesoplodon carlhubbsi* with the pars anteroexternus muscle removed. The posterior fibers of the exposed pars anterointernus sweep across the spiracular surface of the vertex (arrow). In the facial fossa, these fibers fold over the more anterior fibers of the pars anterointernus. Exposed facial border (dark stippled region) is the site of origin of the removed pars anterointernus muscle. AI = pars anterointernus muscle, BH = blowhole, M = melon, RM = rostral muscle.

connective tissue mass around the blowhole. Some dorsal fibers even sweep up over the top of the melon. The most lateral posterior fibers of the lateral rostral muscle insert laterally into the superficial tissue posterior to the gape.

The melon of *Mesoplodon carlhubbsi* is grossly similar to the same structure in delphinoids. The melon is basically composed of loose connective tissue fibers with varying amounts of adipose tissue within it. Typically, the tissue of the melon grades into the connective tissue of the hypodermis along its dorsal and anterior surfaces. The melon is also similar to delphinoids in that the fattiest region, the melon core, tends to be situated asymmetrically slightly toward the right side and extends posteriorly deeply into the right nasal plug but only to a slight extent into the left nasal plug (Mead, 1975a). In a transverse section approximately half-way between the tip of the rostrum and the antorbital notches, the small melon is situated asymmetrically to the right side. The fibers of connective tissue in this region tend to be oriented concentrically, originating from the lateral aspect of the rostrum and extending over the top of the melon region. In a sagittal section, these connective tissue fibers appear to radiate dorsally and anteriorly from the rostrum. Dorsal to the most fatty core of the melon is the region just below the epidermis that is composed of a dense connective tissue matrix. At the antorbital region, the melon is once again situated more to the right side. The most fatty part that has no muscles in it is definitely on the right side.

The tightly drawn blowhole ligaments in *Mesoplodon* spp. are quite different from those in delphinoids, iniids, and platanistids. Each blowhole ligament is attached at the medial notch of the vertex on the premaxilla and its anterior border extends laterally and ventrally to a small tubercle on the lateral edge of the premaxilla on the spi-

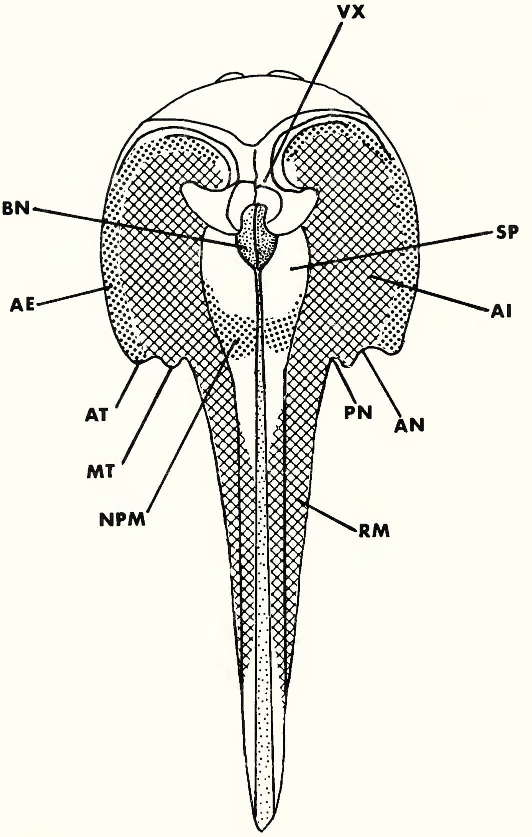


**Figure 8.** Dorsal view of the skull of *M. carlhubbsi* with the origins of the major facial muscles indicated. AE = pars anteroexternus, AI = pars anterointernus muscle, AN = antorbital notch, AT = antorbital tubercle, BN = bony naris, MT = maxillary tubercle, NPM = nasal plug muscle, PN = prominential notch, VX = vertex.

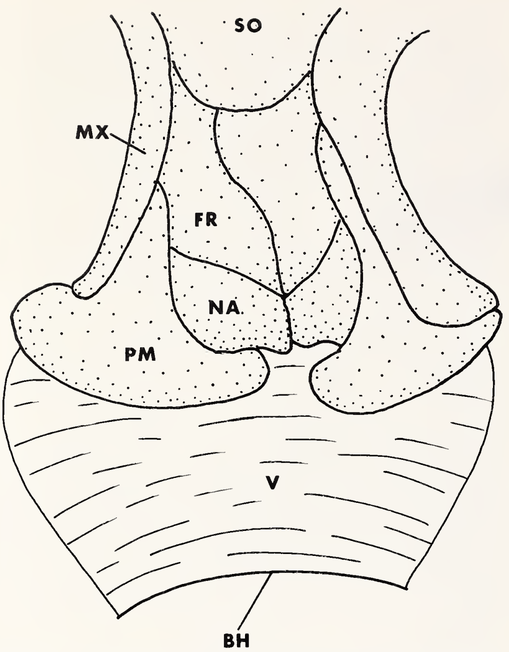


**Figure 9.** Diagrammatic dorsal view of the nasal vestibule of *Mesoplodon stejnegeri* from the blowhole posterior to the vertex of the skull. BH = blowhole, FR = frontal, MX = maxilla, NA = nasal, PM = premaxilla, SO = supraoccipital, V = vestibule.

racular plate (Fig. 5). In young specimens, the blowhole ligament consists solely of fibrous connective tissue, but the adult specimens of *Mesoplodon* that I have dissected had a distinct hyaline cartilage along the leading edge of the ligament. This cartilage may become more prominent with age. Purves and Pilleri (1973) suggested that similar cartilages found in *Platanista* spp. were homologous with the crus lateralis of terrestrial mammals.

The paired nasal plugs are large masses, consisting primarily of connective tissue, with hemispherically shaped posteroventral surfaces. The nasal plugs are situated against the spiracular surface of the vertex and occlude the bony nares ventrally when the nasal plug muscles are relaxed (e.g. Fig. 16). The nasal plugs in *Mesoplodon* are quite large, spreading laterally across the entire spiracular surface of the vertex. Although relatively much larger than the nasal plugs of delphinoids, iniids, and platanistids, they lack the distinct acutely angled lateral edge or lateral lip present in these other odontocetes. The right nasal plug is usually twice the width of the left nasal plug, in correlation with the extreme asymmetry of the cranium in this region. In this feature, *Mesoplodon carlhubbsi* is much more asymmetrical than are delphinoids, iniids, and platanistids. Posteriorly, on the nasal plugs are horizontal creases that correspond with the edges of the blowhole ligaments and presumably result in a very tight fit of the nasal plugs against the spiracular surface of the vertex. As with all other ziphiids that I have dissected, the fatty tissue of the melon extends extensively into the right nasal plug and relatively much less into the left nasal plug. This melon core extends posteriorly almost to the posterior end of the right nasal plug.

Running nearly vertically on the posterior surfaces within the bony nares are paired small folds of tissue that attach dorsally to the medial aspects of the blowhole ligaments; these folds appear to attach also to the medial notch on the vertex (Fig. 5). They may be homologous with the diagonal membranes of delphinoids.

### *Mesoplodon stejnegeri*

There are no detailed published accounts regarding the anatomy of this species. The only reference to the facial anatomy is that by Tomilin (1967) who stated "Spermaceti case ascending gently to the rear of the beak." This reference to a spermaceti case has subsequently been cited (Loughlin and Perez, 1985). I interpret the original statement to describe the external profile of the head. The unfortunate use of the term spermaceti case implies an incorrect homology to that internal structure which is found in physeterids. The homology between facial structures of physeterids and other odontocetes is discussed in the Homology section.

Some previous researchers have felt that *M. carlhubbsi* is conspecific with *M. stejnegeri*. However, consistent cranial differences (Moore, 1963), external differences (Mead et al., 1982), and the differences described below in the facial soft anatomy provide overwhelming evidence that these two species are distinct.

**Nasal Passages.** The blowhole is a wide shallow transverse crescent with anteriorly directed apices. It is situated almost symmetrically, but extends more posteriorly on the left side. The vestibule (Fig. 9) expands laterally deep to the blowhole. This lateral expansion is far more extensive on the right side, making the vestibule more asymmetrical than that found in the other species of *Mesoplodon* examined. At the region of the vertex, the right side is approximately twice the width of the left side in reference to the medial septum. There are no folds or creases along the surfaces of the nasal vestibule, and there is no vestibular sac. The floor of the vestibule is extremely convex on the right side, but only slightly convex on the left. This dorsalward bulging on the right side overlies the melon core.

The posterior nasal sacs (Fig. 10) are similar to those found in other species of *Mesoplodon*. Both sides are adjacent to the spiracular surface of the premaxillae. The right posterior nasal sac is larger than the left, corresponding with the larger surface of the right premaxilla. There is a bilateral pair of anteriorly oriented folds in the posterior surface of the blowhole ligaments that form small diverticula. These diverticula are homologous to the posterior portion of the nasofrontal sacs of delphinids. On the right side, there is a well-developed anterior portion of the nasofrontal sac that curves medially

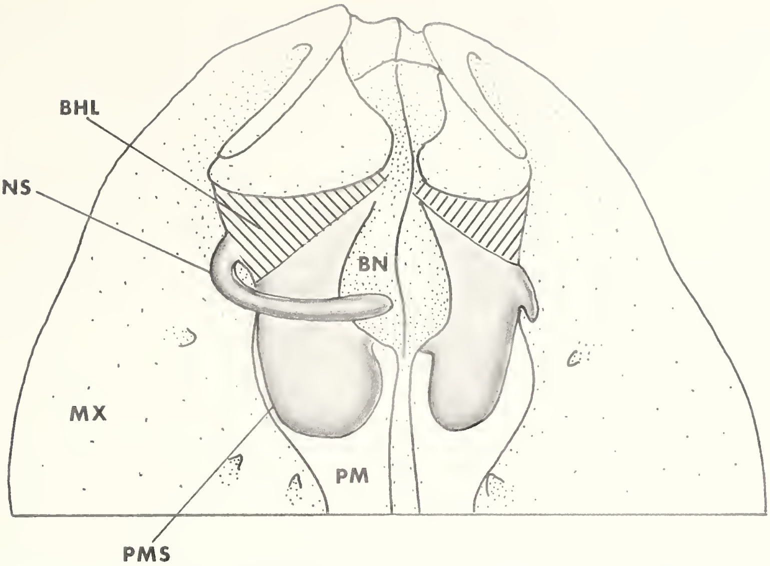


**Figure 10.** Anterodorsal view of the nasal diverticula of *Mesoplodon stejnegeri.* The hatched region represents the position of the blowhole ligaments behind which lie the paired posterior nasal sacs. BHL = blowhole ligament, BN = bony naris, MX = maxilla, NS = anterior section of nasofrontal sac, PM = premaxilla, PMS = premaxillary sac.

into the right nasal plug between the dorsally situated dense connective tissue and the underlying melon core region. The right anterior section of the nasofrontal sac extends medially approximately to the anatomical midline. In the adult specimen, the sac was about 1 cm in diameter. In neither specimen were there traces of a left anterior aspect of the nasofrontal sac. In this feature, *M. stejnegeri* differs from *M. carlhubbsi* in which both a right and left anterior nasofrontal sac are present.

The premaxillary sacs (Fig. 10) were fairly typical in morphology to those found in other species of *Mesoplodon.* In the adult specimen I examined, the premaxillary sacs extended approximately 4 cm anterior to the bony nares. Lateral to the bony nares, the left sac extended approximately 2 cm and the right sac extended about 3.5 cm.

**Soft Anatomy.** In profile, this species has a less pronounced melon region than that of *M. carlhubbsi* (Tomilin, 1967; Mead et al., 1982). The blubber layer and superficial fascial layers are similar to those found in other species of *Mesoplodon.* The blubber layer easily separates from the facial muscles within the facial fossa posterior to the level of the blowhole. Anterior to the blowhole, the blubber tissue grades into the underlying fat and connective tissue.

The two main muscles of the facial fossa, the pars anteroexternus and the pars anterointernus, were not carefully dissected. However, they appeared grossly to be similar to those muscles described for *M. carlhubbsi.*

The rostral muscle originates anteriorly along the rostrum to a point immediately posterior to the level of the teeth, at approximately 25 cm posterior to the tip of the rostrum. It continues as an undifferentiated muscle for about 20 cm posteriorly that originates from the lateral aspect of the rostrum and extends dorsolaterally into the connective tissue and blubber layer. In this region some fibers of the rostral muscle originate off the dorsal surface of the mandibles similar to the condition found in *M. densirostris.* In a transverse section about 50 cm posterior to the rostral tip, the rostral muscle becomes differentiated, with the most laterally originating fibers extending ventrolaterally and the rest of the fibers extending concentrically into, and dorsal to, the melon.

The melon is a long ovoid mass that extends from about the posterior edge of the teeth to the right nasal plug. Anteriorly, it has loose transverse sheets of connective tissue that are oriented in an anterodorsal plane. The melon reaches its greatest width just anterior to the antorbital notch and is slightly larger on the right side than on the left. Posterior to this, the melon tapers asymmetrically to the right side extending to the posterior surface of the right nasal plug.

The blowhole ligaments were similar in position and shape to those structures found in *M. carlhubbsi.* They extend ventrolaterally across the premaxillae at about a 45° angle. They are tightly appressed against the spiracular surface and contain a section of hyaline cartilage within their leading edge. There are small, paired transverse creases along the anterior surface of the blowhole ligaments that correspond to ridges on the posterior surface of the nasal plugs.

The gross morphology of the paired nasal plugs is similar to that of structures in *M. carlhubbsi.* The right plug is filled primarily with the white fatty tissue of the melon core that extends to the pos-

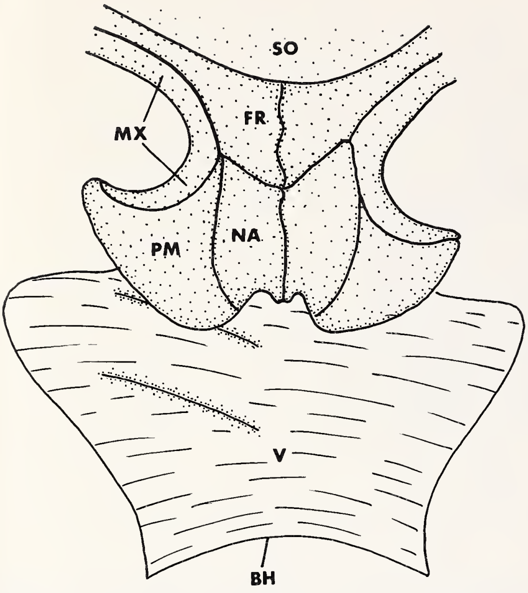


**Figure 11.** Dorsal view of the floor of the nasal vestibule of *Mesoplodon bidens*. There are two distinct grooves evident on the floor of the vestibule only on the right side. BH = blowhole, FR = frontal, MX = maxilla, NA = nasal, PM = premaxilla, SO = supraoccipital, V = vestibule.

terior surface of the nasal plug. Within the ventral portion of the right nasal plug are loose bundles of the nasal plug muscle. This muscle originates from the right premaxilla and inserts into the tissue of the nasal plug in a posterodorsal and slightly medial plane. The left nasal plug is slightly smaller than the right and is filled with the relatively and absolutely larger left nasal plug muscle. The left nasal plug muscle originates more extensively off the left premaxilla and its fibers are oriented in the same manner as the right nasal plug muscle.

### *Mesoplodon bidens*

This is the only species of *Mesoplodon* for which the facial anatomy has been described in the literature. Schenkkan (1973) described the anatomy based on his dissections of two specimens. I secured one specimen for dissection and will compare my findings with Schenkkan's.

*Mesoplodon bidens* is notable among the species of *Mesoplodon* in that the head is relatively narrow and gracile, with a relatively long rostrum. The other species of *Mesoplodon* with a narrow head with a long rostrum are *M. grayi* and *M. layardi*, both of which are Southern Hemisphere species. It is not at all clear whether this superficial resemblance is due to evolutionary relationship or to parallelism, although a similar and derived mandibular tooth position is shared by the three species.

**Nasal Passages.** The position and shape of the blowhole is typical for species of *Mesoplodon*. It is a shallow transverse lunate slit with anteriorly directed apices. It is situated slightly off to the left side, and the right apex is set slightly in front of the left. The vestibule (Fig. 11) of the nasal passage extends posteriorly and ventrally towards the spiracular surface of the vertex at a 45° angle form the horizontal. Schenkkan (1973) noted that the floor of the distal nasal passage on the right side was convex but not on the left side. The entire ventral aspect of the distal nasal passage was convex in the specimen that I dissected. For the first few cm deep to the blowhole, the nasal passage does not widen laterally, but thereafter it expands to extend well beyond the lateral edge of the vertex (Fig. 11). On the right floor of the vestibule are two transverse creases oriented anteriorly and medially. The most anterior crease is about 7 cm in length and has a maximum depth of 15 mm. The smaller posterior crease is slightly over 5 cm in length and less than 1 cm deep.

The vertex and the spiracular surface in this species are relatively small in comparison to those in other species of *Mesoplodon*, and the corresponding nasal plugs and sacs are also comparatively small. The blowhole ligaments are small and consist of two connective tissue folds invested with hyaline cartilage along their ventral borders. These ligaments extend from the medial notch of the vertex to a small boss on the lateral edge of the premaxillae. The leading edge of each ligament is tightly appressed to the spiracular surface of the vertex, but dorsal to this the tissue is more flaccid, with a wrinkled posterior surface that presumably allows for expansion of the posterior nasal sacs. These posterior nasal sacs are similar in shape to those found in *Mesoplodon carlhubbsi;* however, they extend dorsally along the spiracular surface of the vertex for only about 1 cm, which makes them relatively small for *Mesoplodon*. The apertures of the small accessory sacs are about 1 cm in width and are located at the lateral edges of the blowhole ligaments. These sacs appear cylindrical, whereas most of the other nasal sacs are flattened. Schenkkan (1973) reported that he did not find accessory sacs in his specimens. Because these sacs are short and open widely, it is possible that he did not consider these outpocketings to be homologous with the more discretely formed accessory sacs of delphinids.

The anterior components of the nasofrontal sacs are present in *M. bidens*. The left anterior aspect of the nasofrontal sac is a small laterally compressed diverticulum that extends only about 1 cm medially. It originates at about midlevel from the bony nares. The right anterior aspect of the nasofrontal sac is round in cross section with a distinctly wrinkled surface indicating that it is fairly distensible. It extends medially approximately 2 cm into the right nasal plug. Its aperture to the nasal passage is situated higher than that of the left sac, about two-thirds of the way dorsally on the bony nares. Schenkkan (1973) noted that the right anterior portion of the nasofrontal sac was about twice as large

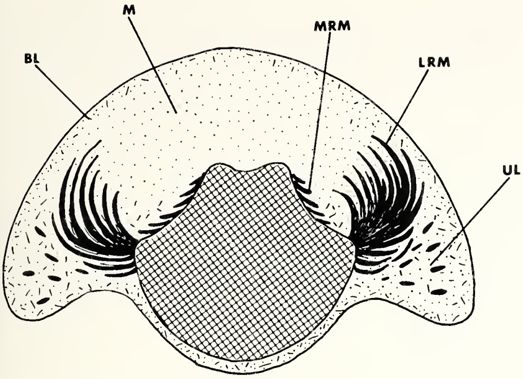


**Figure 12.** Cross section, looking posteriorly, through the rostrum of *Mesoplodon bidens* at ¼ the rostral length anterior to the antorbital notches. Note the lack of dense connective tissue dorsal to the melon in this region. BL = blubber, LRM = lateral rostral muscle, M = melon, MRM = medial rostral muscle, UL = upper lip.

as that of the left sac and that P.E. Purves had stated to him that an old male *M. bidens* he had dissected lacked the left sac altogether. The premaxillary sacs are similar in shape, symmetry, and position to those found in *M. carlhubbsi.*

**Soft Anatomy.** The pars anteroexternus is covered with a few layers of superficial fascia in the region of the facial fossa. The origin and insertion of this muscle are quite similar to the pattern found in *M. carlhubbsi,* but the muscle was only about 5 mm thick in the specimen that I dissected. Deep to this muscle is the larger pars anterointernus that is similar to its counterpart in *M. carlhubbsi.* The origin of the pars anterointernus is virtually the entire surface of the facial fossa immediately deep to the pars anteroexternus. The pars anterointernus has a broad insertion on the connective tissue surrounding the nasal vestibule except for the most posteriorly originating fibers that fold medially across the spiracular surface of the vertex. This is clearly figured by Schenkkan (1973). A supraorbital muscle originates from the supraorbital process with longitudinally oriented fibers that insert onto the dense connective tissue mass at the antorbital region. This muscle, which I have found in all the species of *Mesoplodon* that I have dissected, is figured, but not labeled or discussed, by Schenkkan (1973:fig. 6) for *M. bidens.*

In correlation with the length of the rostrum, the origins of the various sections of the rostral muscles are quite long, beginning approximately one-third of the way back from the tip of the rostrum and merging caudally with the fibers of the pars anterointernus. Anteriorly, the muscle is simple and distinctly separated into medial and lateral parts (Fig. 12). In a cross section at the level of the antorbital notches, there are three components to the rostral muscle. Most medially is a small portion that lies in the trough formed by the lateral edge of the premaxillae (Fig. 13). Its fibers are directed dorsally and medially along the premaxillae and insert on the connective tissue on the dorsal surface of the rostrum. The next muscle is separated from the previous by a wedge of fatty tissue attached to the lateral edge of the maxilla. This muscle originates from the lateral edge of the maxilla and has fibers

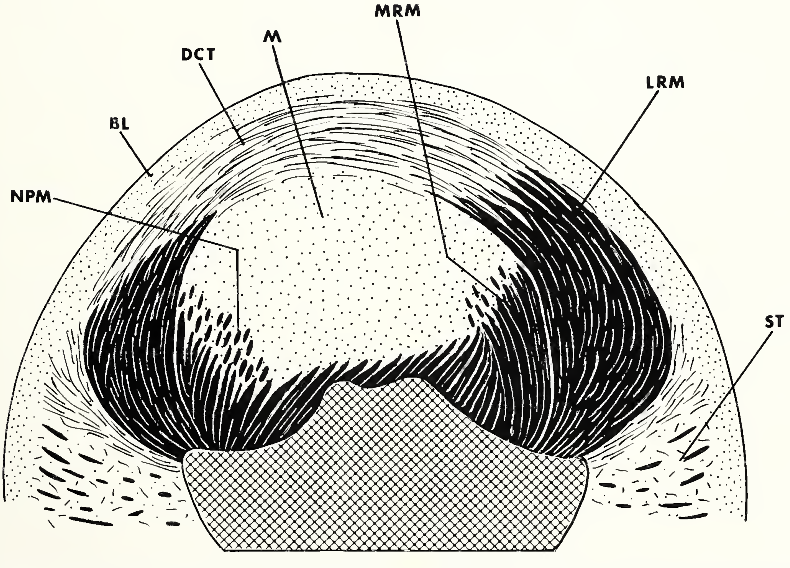


**Figure 13.** Cross section, looking posteriorly, through the rostrum of *Mesoplodon bidens* at the level of the antorbital notches. Note that there is a layer of dense connective tissue fibers dorsal to the melon. The melon is distinctly offset to the right in this region, and the nasal plug muscle is larger on the right. BL = blubber, DCT = dense connective tissue, LRM = lateral rostral muscle, M = melon, MRM = medial rostral muscle, NPM = nasal plug muscle, ST = superficial tissue at angle of mouth.

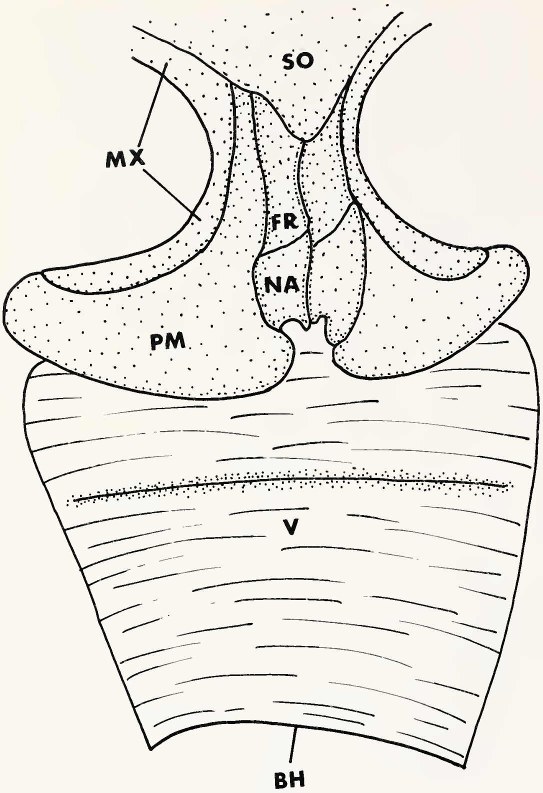


**Figure 14.** Dorsal view of the floor of the nasal vestibule of *Mesoplodon densirostris* (SBMNH 3138). Note that in this specimen, there is a single transverse groove in the floor of the vestibule. BH = blowhole, FR = frontal, MX = maxilla, NA = nasal, PM = premaxilla, SO = supraoccipital, V = vestibule.

that spread laterally and then sweep diffusely dorsally into the melon. The third muscle is immediately ventral and lateral to the above. This muscle is quite diffuse within loose connective tissue and fat. This muscle and its matrix constitute the superficial tissue posterior to the gape of the mouth (Fig. 13), which is well developed in specimens of *Mesoplodon* (Mead et al., 1982; Heyning, 1984).

The nasal plug muscles are small. They originate from the premaxillae just anterior to the premaxillary sacs. These muscles have quite diffuse fibers that insert anteriorly and dorsally into their respective nasal plugs. The connective tissue fibers within the melon and subdermally along the anterior aspect of the facial region appear to be less dense than in most other *Mesoplodon* specimens dissected. Because I was able to dissect only one young male specimen of *M. bidens,* it is not clear whether this feature is typical for the species or due to the immaturity of this specimen. The fatty tissue of the outer sheath of the melon that contains relatively more connective tissue than the inner core is quite extensive. It extends continuously throughout the length of the rostrum. The core of the melon is typical in position, set asymmetrically off to the right side, and extends into the right nasal plug much more extensively than into the left. Schenkkan (1973) figured and discussed the presence of a "globular mass of adipose tissue which was clearly independent of the melon" dorsal to the right premaxillary sac. This is in the exact position of the enlarged core of the melon that extends posteriorly into the right nasal plug. This feature is prominent in all ziphiid specimens that I have dissected. Unless his specimen was anomalous, I believe that this is what Schenkkan was describing and that his statement that it was independent of the melon is incorrect.

### *Mesoplodon densirostris*

The facial region of *Mesoplodon densirostris* is unique among the species of *Mesoplodon* in that the rami of the mandibles curve sharply dorsally. This brings the gape up to or, in the case of adult males, above the level of the flattened melon region in this species (Leatherwood et al., 1982). In adult males, the erupted teeth are situated on top of the elevated aspect of the mandible and project well above the head (Heyning, 1984).

**Nasal Passages.** The blowhole is similar to those in the other *Mesoplodon* species with its moderately deep transverse crescent with rostrally pointed apices. The nasal vestibule gradually widens posteriorly until it reaches the spiracular surface of the vertex, where its lateral edges project slightly beyond the spiracular surface (Fig. 14). The blowhole is situated relatively far in front of the vertex compared to the position in other species of *Mesoplodon* that I have dissected. This anterior position of the blowhole is related to the shallow angle of the nasal vestibule that lies at approximately 30° from the horizontal. The vestibule is lined with smooth epithelium that is darkly pigmented near the blowhole, but deeper it becomes pinkish in color in patches. There are often transverse grooves in the anteroventral floor of the nasal vestibule that extend the entire width of the nasal passage (Fig. 14). These grooves vary considerably among specimens. In one female, there was a nearly straight groove two-thirds of the distance in from the blowhole. In another female there were three grooves whose lateral aspects curved posteriorly. No vestibular sac was found in any of the specimens dissected.

Paired posterior nasal sacs (Fig. 15) extend dorsad from beneath the blowhole ligaments. Both sacs are situated against the spiracular surfaces of the premaxillae, although the right sac has a small dorsal pocket that extends laterally approximately 1 cm beyond the bony surface. On both sides there are very small outpockets just posterior to the lateral insertions of the blowhole ligaments; these are the rudimentary accessory sacs.

The anterior components of the nasofrontal sacs found in all other species of *Mesoplodon* examined were absent in most specimens of *M. densirostris* that I dissected. The exception was an adult male

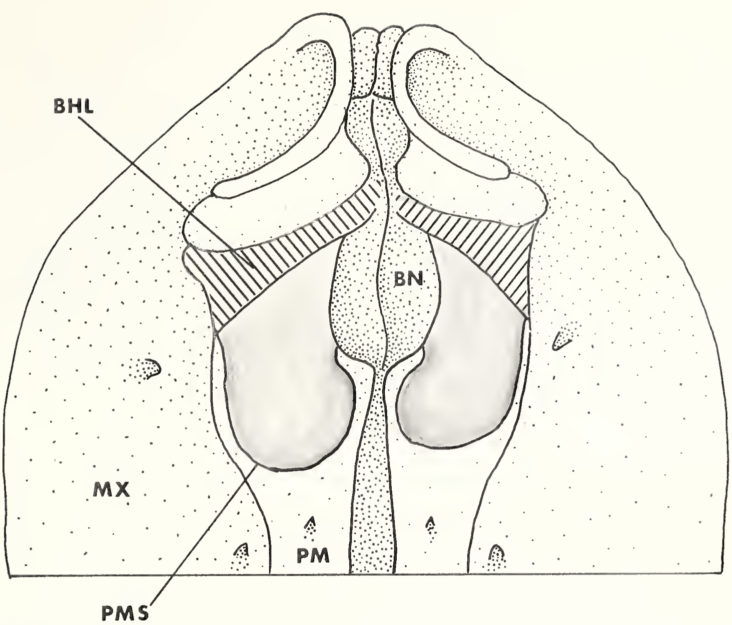


**Figure 15.** Diagrammatic anterodorsal view of the blowhole ligaments and an outline of the underlying posterior nasal sacs in *Mesoplodon densirostris* (USNM 550338). The anterior sections of the nasofrontal sacs are lacking in this species and the posterior nasal sacs are completely covered in this view by the blowhole ligaments (hatched region). BHL = blowhole ligament, BN = bony naris, MX = maxilla, PM = premaxilla, PMS = premaxillary sac.

(USNM 550754) that had a 1-cm-long nasofrontal sac on the right side that curved slightly anteriorly. This sac was tubular in cross section, and the internal surface was wrinkled. There was no nasofrontal sac on the left side of this specimen.

The premaxillary sacs are similar to those of other species of *Mesoplodon,* except that the apertures to the narial passages are only along the lateral portion of the bony nares. Along the anterior aspect of the bony nares are a bilateral pair of small transverse folds of tissue that connect medially with the medial septum and occlude the posteromedial aspect of the premaxillary sacs. The premaxillary sacs do not extend anteriorly to the margin of the spiracular plate when empty; however, by palpation it is clear that, when they are filled with air, they can be distended to this point. The right sac extends anteriorly approximately as far as the left sac, but the right sac is about twice as wide.

**Soft Anatomy.** There are several layers of superficial fascia in the facial region, but the orientation of the fibers and the number of discrete layers were difficult to determine. It appeared that, at least in one male specimen, there were some scattered muscle fibers within the superficial fascia.

The supraorbital muscles originate from the facial border lateral to the pars anteroexternus muscles just above the temporal fossa and insert onto the dense connective tissue blocks along the supraorbital ridges. The supraorbital muscle is approximately 1 cm thick and 4–6 cm long.

The pars anteroexternus is a broad, flat muscle that is about 1 cm thick and originates along the facial border from the supraorbital region back to the vertex. In some specimens, the origin extended along the narrow sagittal surface of the vertex. Its fibers converge on the posterior and lateral aspects of the connective tissue surrounding the blowhole. Its posterior fibers are oriented anteriorly and extend over the lateral edges of the vertex of the skull.

The pars anterointernus is a larger muscle that originates broadly within the facial fossa. The anterior fibers are oriented dorsomedially and insert onto the anteroventral portion of the nasal vestibule. The more lateral and posterior fibers insert onto the posterodorsal aspect of the vestibule. Because the vestibule is angled forward at about 30° from the horizontal, the lateral and posterior fibers of the pars anterointernus fold over some of the more anterior fibers where they meet. The most posterior fibers of the pars anterointernus converge medially across the spiracular surface of the vertex, much as they do in other species of *Mesoplodon.*

The rostral muscles of this species are more developed than in other species of *Mesoplodon* that I have dissected (Figs. 17, 18). The origin of the rostral muscles extends anteriorly on the rostrum to approximately one-fourth to one-third the length from the tip. The anterior fibers are not differentiated into lateral and medial components and are oriented primarily dorsally, inserting into dense connective tissue. Approximately 30 cm from the rostrum tip, distinct lateral and medial rostral muscles can be distinguished; both of them are interspersed within a white fatty matrix. More posteriorly, the medial rostral muscle inserts onto the

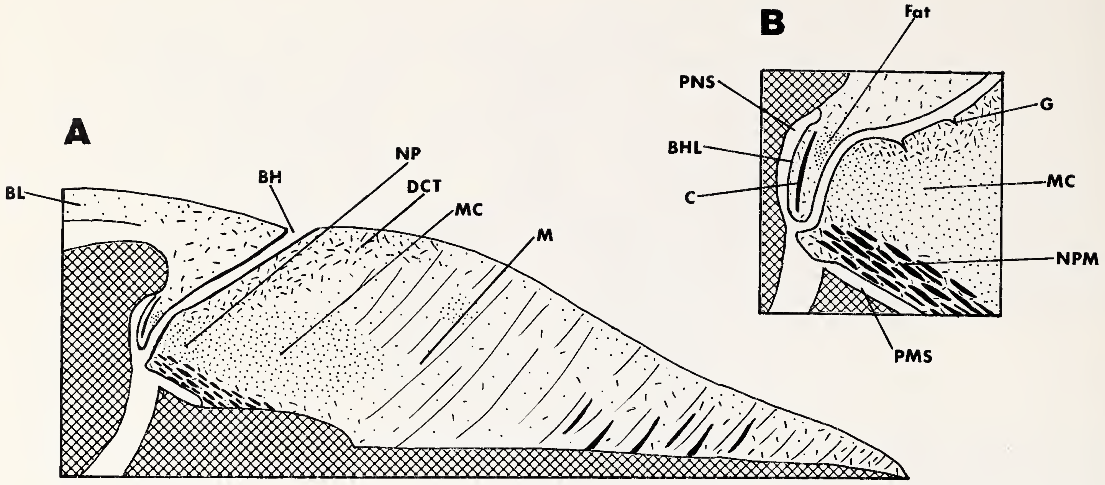


**Figure 16.** **A,** Diagrammatic parasagittal section through the right naris of *Mesoplodon densirostris* (USNM 550746). **B,** Enlargement of the narial region. Note that the fatty tissue of the melon core can be found along the anterior aspect of the blowhole ligament in this section. BH = blowhole, BHL = blowhole ligament, BL = blubber, C = cartilage in blowhole ligament, DCT = dense connective tissue, G = groove, M = melon, MC = melon core, NP = nasal plug, NPM = nasal plug muscle, PMS = premaxillary sac, PNS = posterior nasal sac.

ventral aspect of the melon, whereas the lateral rostral muscle inserts adjacently on the lateral aspect of the melon. No muscle fibers pass dorsally over the top of the melon on the rostrum. In the antorbital region, most of the fibers of the medial rostral muscle insert onto the ventrolateral aspect of the melon. However, some of the more laterally originating fibers do sweep over the top of the melon, completely encircling it. The posterior aspect of the lateral muscle fibers inserts onto the blubber layer near the angle of the mouth. This part of the lateral rostral muscle is larger in *M. densirostris* than in other species of this genus that I have examined.

Anteriorly on the rostrum, there is more dense connective tissue and less fat than in other species of *Mesoplodon* and in *Ziphius cavirostris.* The fat of the melon becomes distinguishable approximately 15–20 cm posterior to the rostrum tip. The anterior aspect of the melon of females is similar in general to what is seen in other species of *Mesoplodon,* except that the rostrum is somewhat rectangular in cross section. In the adult male, the anterior melon is partially divided longitudinally by a dorsomedial cleft of dense connective tissue (Fig. 17). In this region, the blubber layer of the adult male contains extensive amounts of connective tissue as compared to adult females. This additional connective tissue may provide protection and/or cushioning when males fight. I previously hypothesized (Heyning, 1984) that intraspecific aggression occurs by a male rubbing the dorsal surface of its head against another male, raking it with the exposed mandibular teeth. In a cross section 30 cm from the rostrum tip, the fatty melon can be seen and is situated almost symmetrically in the rostrum. It appears as a dorsally flattened mass situated directly on the rostrum with the lateral rostral muscle fibers inserting onto its ventrolateral surface. Dorsolaterally, the melon is surrounded by dense connective tissue that blends into the blubber superficially. Approximately 40 cm from the rostral tip, the fatty core of the melon is distinctly displaced off on the right side (Fig. 18). On the left of the core is the region of the melon containing more connective tissue. The combined regions of the melon lie immediately dorsal to the bones of the rostrum and are relatively symmetrical in position. There are relatively fewer connective tissue fibers in the noncore region of the melon of *M. densirostris* than in other species within the genus.

The blowhole ligaments are similar to those of other species of *Mesoplodon* in gross appearance (Figs. 15, 16). They angle ventrolaterally along the spiracular surface of the vertex at approximately 45° on the right, and slightly more vertically on the left. Within the leading margins of the blowhole ligaments are the paired irregularly shaped cartilages that give them rigidity (Fig. 19). In one specimen, a longitudinal section through the right nasal plug and blowhole ligament revealed, anterior to the cartilage of the blowhole ligament, a region of clear fat similar to the melon core tissue. It was positioned adjacent to the region of the right nasal plug where the melon extends most posteriorly. With the nasal vestibule in its normal closed position, these two regions of fat are in direct contact with each other. It is unclear, however, whether or not this pattern is typical for all specimens of this species or even the entire family because I did not find this structure until my later dissections, and may have overlooked it previously. This fatty structure is probably homologous to the similar structure found in delphinids referred to as the elliptical body (Mead, 1975a).

The nasal plugs are similar to those found in

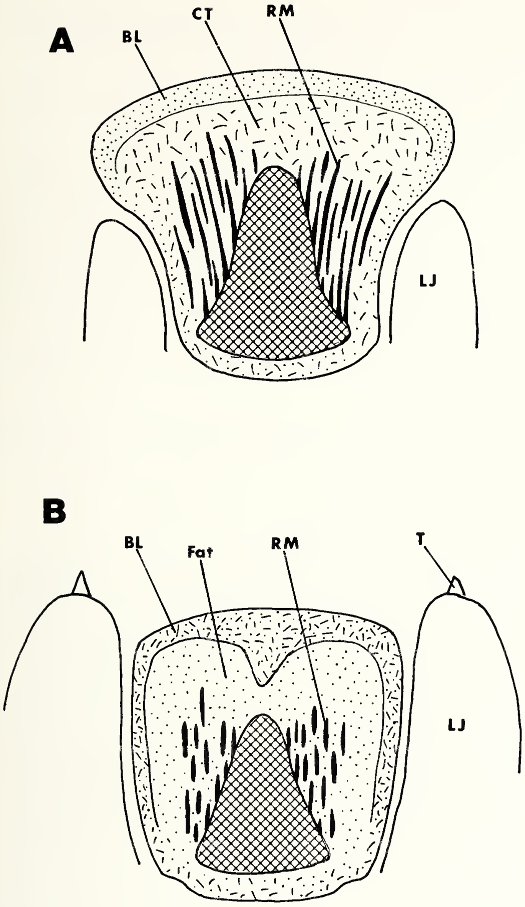


**Figure 17.** Cross sections, looking posteriorly, through the rostrum of an **A,** adult female (SBMNH 3138) and **B,** adult male (USNM 550754) *Mesoplodon densirostris* at the level of the teeth approximately 25 cm behind the rostral tip. The outline of the lower jaws is indicated lateral to the rostrums and the erupt teeth of the male can be seen on the apex of the lower jaws. In the male, the blubber layer contains a great amount of connective tissue fibers. BL = blubber, CT = connective tissue, LJ = lower jaw, RM = rostral muscle, T = tooth.

other species of *Mesoplodon* except that they are relatively smaller in correlation with the smaller vertex found in this species. As with other ziphiids examined, the melon extends posteriorly into the right nasal plug, whereas the left nasal plug is filled with connective tissue and nasal plug muscle.

At 45 cm from the tip of the rostrum, the enlarged right nasal plug muscle is clearly evident and occupies a large portion of the area corresponding to the melon on the left side. Both nasal plug muscles originate anterior and lateral to the respective premaxillary sacs.

### *Hyperoodon ampullatus*

Unfortunately, I was not able to secure a specimen of this species or the Southern Hemisphere species *H. planifrons* to dissect and must therefore rely upon published accounts of the facial anatomy of the north Atlantic species (Carlsson, 1888; Kükenthal, 1893; Schenkkan, 1973). These descriptions are briefly reviewed here. A major feature of the facial region of the skull in *Hyperoodon* spp. is the great dorsalward expansion of the maxillary ridges often termed the maxillary crests. These maxillary crests increase in size allometrically with age and are considerably more developed in adult males

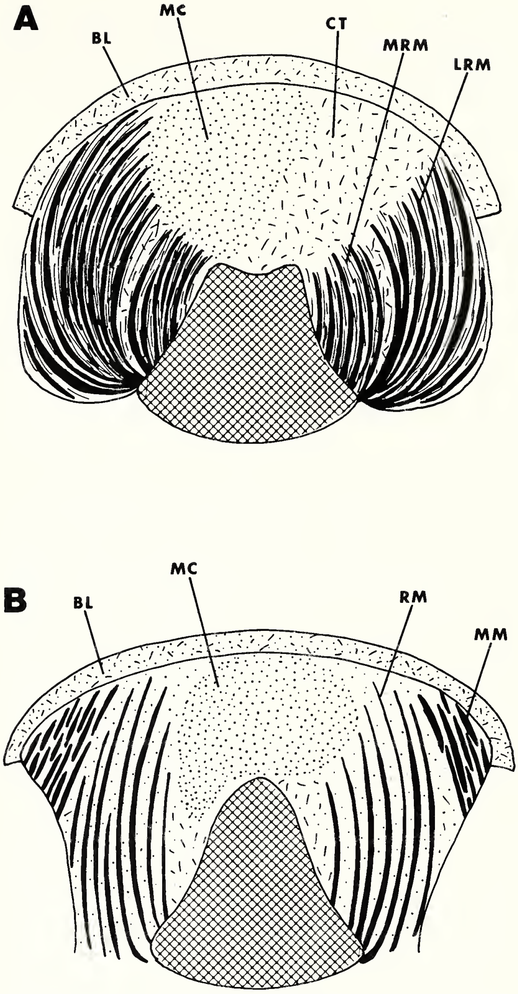


**Figure 18.** Cross sections, looking posteriorly, through the rostrum of an **A,** adult female (SBMNH 3138) and **B,** adult male (USNM 550754) *Mesoplodon densirostris,* just anterior to the antorbital notches. The blubber layer is removed laterally. In both sexes, the melon is asymmetrically situated off to the right side. Note the dimorphism in the lateral rostral muscle and the overall shape of the rostrum. In the male, there are some muscle fibers (MM) that originate from the mandibles (not shown) and insert laterally onto the blubber layer. BL = blubber, CT = connective tissue, LRM = lateral rostral muscle, M = melon, MC = melon core, MRM = medial rostral muscle, RM = rostral muscle.

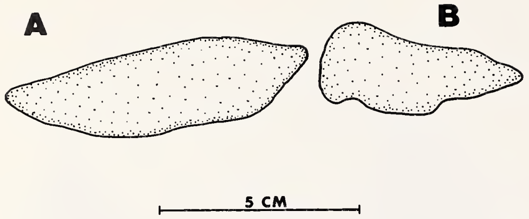


**Figure 19.** **A,** Right; and **B,** left anterior views of the hyaline cartilages found in the blowhole ligaments of *M. densirostris* (USNM 550338). Note the size difference and irregular shapes.

(Gray, 1882). The vertex is of a construction similar to that of *Mesoplodon* spp., with lateral flanges on the anterior aspect and small nasals that are situated in a median notch.

**Nasal Passages.** The blowhole of this species is reported to be displaced toward the right side. It appears as a shallow transverse slit with the typical odontocete pattern of forwardly directed apices. The vestibule of the nasal passage extends posteriorly and ventrally to the spiracular surface of the vertex as a dorsoventrally flattened tube that expands laterally toward the vertex. The blowhole ligament seems to be at least grossly of the same general pattern as found within the genus *Mesoplodon.* The sacs posterior to the blowhole ligament are described as being partially divided into anterior and posterior compartments by a ventrally protruding flap of tissue. This description is similar to the condition I found in *Berardius bairdii*, iniids, monodontids, and phocoenids, and descriptions in the literature of platanistids. Thus, the anterior compartment is homologous to the posterior nasofrontal sac, and the posterior compartment is homologous to the posterior nasal sac found in other odontocetes. Kükenthal's parasagittal section of *H. ampullatus* (1893:pl. XXII, fig. 9) is very similar to the morphology I found in *B. bairdii* (see Fig. 29). Kükenthal used the term "hintere obere Nebenhohle" for both the posterior nasal sac and the posterior nasofrontal sac as used herein. In Schenkkan's specimen of *Hyperoodon ampullatus,* there were no anterior components to the nasofrontal sacs present, nor were accessory sacs found. The premaxillary sacs are described as similar to those in *Mesoplodon bidens.*

**Soft Anatomy.** Schenkkan (1973) did not provide details regarding the facial musculature. He did state, however, that the enlargment of the maxillary crests is correlated with a change in the angle of orientation of some of the facial muscles. His figure 8 indicates that the posterior part of the pars anterointernus is similar to that found in other ziphiids. The anterior aspects of the pars anterointernus and rostral muscles have complicated origins from the maxillary crests.

The nasal plugs are described as elongate dorsoventrally with the right plug twice as large as the left. Schenkkan's figure 16 indicates that they lack lateral lips. The melon is described and illustrated as longitudinally elongate and situated between the maxillary crests.

The melon region of females is said to contain a colorless oil, whereas the melon region of males contains a solid elongate mass of fat that is about "twice the size of a large water-melon" (Gray, 1882). Ohlin (1893) described the melon of young animals as consisting of fibrous cells filled with a clear oil; however, old males, called "toendebunds," have a melon made of a dense fibrous tissue mass. It appears that both the size of the bony maxillary crests and the density of the connective tissue fibers within the melon increase with age in the males of this species.

It is clear that more research is needed on this genus of beaked whales to provide details of the facial anatomy.

### *Ziphius cavirostris*

The skulls in this species are extremely sexually dimorphic in the facial region. As is typical for many species of ziphiids, the mesorostral canal of mature males becomes filled with dense bone (Fraser, 1942; Heyning, 1984). *Ziphius cavirostris* differs from other ziphiids in that this filling of the mesorostral canal occurs only in the distal half and corresponds with the simultaneous ontogenetic resorption of bone on the dorsal surface of the facial region anterior to the bony naris. This phenomenon produces the prenarial basin in adult males. This sexually dimorphic anatomical feature is unique to *Z. cavirostris* among extant ziphiids. Due to the extreme sexual dimorphism in the facial anatomy of *Z. cavirostris,* I describe first the anatomy of the young of both sexes and of adult females, and then describe the differences found in adult males. Sexual dimorphism in the facial anatomy is rare among other odontocetes, but it has been described in the delphinid genera *Globicephala* and *Pseudorca,* in which old males develop a more pronounced melon (Mead, 1975a). Male sperm whales (*Physeter catodon*) also have relatively larger facial regions than females, due primarily to an elongation of the soft structures anterior to the tip of the rostrum (Nishiwaki et al., 1963).

As seen in dorsal view (Fig. 20), the elongate nasals extend anterolaterally to the left, and both premaxillae flare laterally. This produces clefts anteriorly on the vertex between the nasals and the premaxillae. Due to the leftward deflection of the nasals, the cleft on the right side is much larger. These clefts are filled with dense connective tissue and hyaline cartilage in life and form a continuous anterodorsal shelf on the vertex.

#### Adult Female

**Nasal Passages.** The blowhole is typical in general shape for odontocetes—a moderately shallow crescent with forwardly directed apices. It is almost symmetrical in position, set only slightly off center toward the left side. The vestibule of the blowhole (Fig. 20) is directed posteroventrally at approximately 45° from the horizontal plane on the right and 35° on the left side. This accounts for observations that the blow of this species is directed anteriorly (Backus and Schevill, 1961; Leatherwood et al., 1982). As the vestibule extends deep, it expands laterally until it reaches the spiracular surface of the vertex below the overhanging anterior aspect of the nasals and premaxillae. As in species of *Mesoplodon,* the lateral expansion of the nasal vestibule is more pronounced on the right side. On the mesethmoid along the spiracular surface of the vertex is a medial ridge of soft tissue, the nasal septum, that partially divides the nasal passage from approximately half-way down the spiracular surface ventrally to the bony nares where the passages are completely divided. This ridge of tissue is also found in most other odontocetes but is less developed.

Passing behind the blowhole ligament and extending dorsally along the spiracular surface of the vertex on the right side is the posterior nasal sac (Figs. 21, 32). On the left side the posterior nasal sac is sometimes absent or vestigial, but the blowhole ligament can always be palpated beneath the tissue along the spiracular surface. This left ligament is similar in position to the blowhole ligament found in males. There are no well-defined accessory sacs or anterior components of the nasofrontal sacs. On the enlarged right side, the right posterior nasal sac extends broadly dorsally and anteriorly along the spiracular surface; it also extends around the anterior surface of the vertex at the region of the connective tissue that fills the bony cleft between the right premaxilla and nasal. This sac terminates as a rounded pocket on the dorsal surface of the vertex several cm posterior to the front edge. The lateral edge of this sac reaches the lateral notch on the premaxilla adjacent to where the deepest fibers of the pars anterointernus sweep around the spiracular surface of the vertex.

The paired premaxillary sacs (Figs. 21, 24) are also extremely asymmetrical in size and shape. The left sac is a small blind pouch lined with loose wrinkled epithelium. This sac is situated primarily about 2 cm lateral to the bony nares but extends anteriorly to approximately 2 cm in front of the edge of the bony nares. The aperture of this sac is approximately 3 cm wide. The right premaxillary sac is many times larger than the left. It extends approximately 5 cm laterad from the margin of the bony nares and anteriorly at least 8 cm. The ventral surfaces of both premaxillary sacs lie adjacent to the bony surfaces of the premaxillae.

**Soft Anatomy.** The thickness of the hypodermis varies considerably from area to area. The blubber tends to be quite thin, only about 1 cm thick in areas with closely underlying bone such as the supraorbital process and the vertex. In the area surrounding the blowhole and anteriorly on the melon, the connective tissue underlying the hypodermis interweaves with the connective tissue of the melon, making clear differentiation impossible. The superficial fascia in the region of the facial fossa is rather diffuse but may be roughly differentiated into three layers. The first consists of fibers that are oriented anteriorly and ventrally. The medial layer has fibers that are more diffuse but are primarily arranged vertically. The fibers of the deepest layer run parallel to the underlying muscle fibers of the pars anteroexternus.

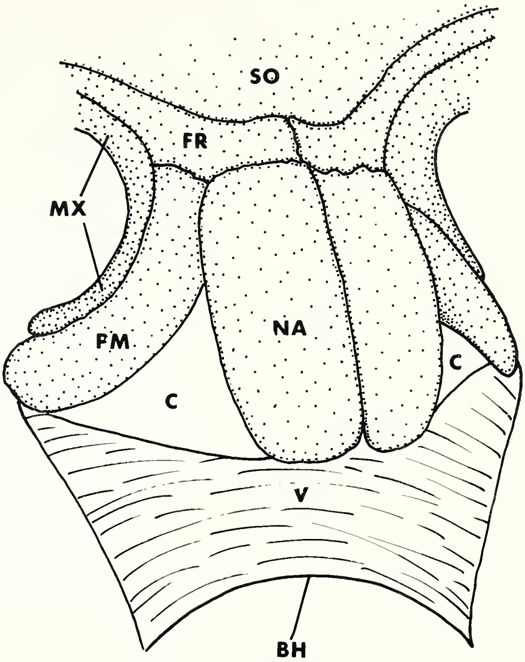


**Figure 20.** Dorsal view of the floor of the nasal vestibule of *Ziphius cavirostris.* Note the enlarged nasals and the thick bands of cartilage that fill the clefts between the nasal and premaxilla bones. BH = blowhole, C = cartilage, FR = frontal, MX = maxilla, NA = nasal, PM = premaxilla, SO = supraoccipital, V = vestibule.

There is no evidence of a pars intermedius or pars posteroexternus muscle. The most superficial muscle in the region of the facial fossa is the pars anteroexternus (Fig. 22), which is a broad and relatively thin muscle that averages about 1–1.5 cm in thickness. It originates along almost the entire facial border primarily from the region of contact of the maxilla and frontal and from the supraorbital region back to the junction of the facial border and the vertex. It inserts diffusely into the thick dorsal aponeurosis that surrounds the blowhole (Fig. 22).

Deep to this is the pars anterointernus. This complex multipennate muscle originates from the maxilla over the entire facial fossa. The insertions of the majority of the fibers of this muscle are on the lateral and posterior portions of the nasal passage deep to the blowhole region. The most posterior fibers that originate from the lateral aspect of the vertex and the posterior aspect of the facial fossa fold over themselves as they sweep below the notch

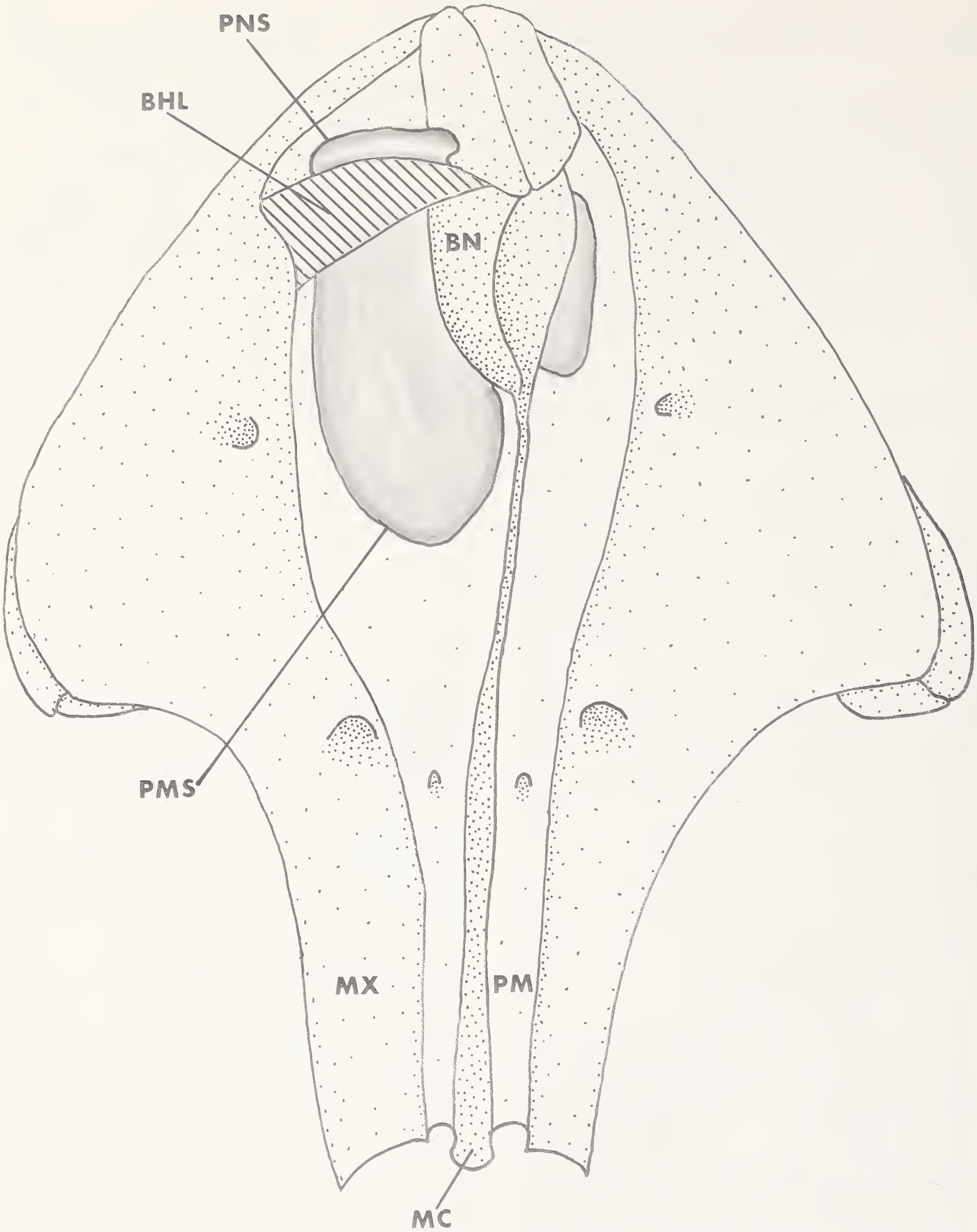


Figure 21. Diagrammatic anterodorsal view of the nasal diverticula of a female *Ziphius cavirostris* (USNM 550779). Most of the right posterior nasal sac is behind the blowhole ligament (hatched region). Note the marked asymmetry of the premaxillary sacs. BHL = blowhole ligaments, BN = bony naris, MC = mesorostral canal, MX = maxilla, NA = nasal, PM = premaxilla, PMS = premaxillary sac, PNS = posterior nasal sac.

lateral on the spiracular plate of the vertex and insert with the corresponding muscle from the other side along the anterior surface of the spiracular surface (Fig. 23). Thus, this muscle covers the blowhole ligaments and posterior nasal sacs. The pars anteroexternus and internus of the specimens of *Ziphius* that I have dissected were less differentiated from one another than were the homologous muscles that I examined in specimens of *Mesoplodon.*

In most dissections, I was able to find some concentric muscle fibers within the connective tissue

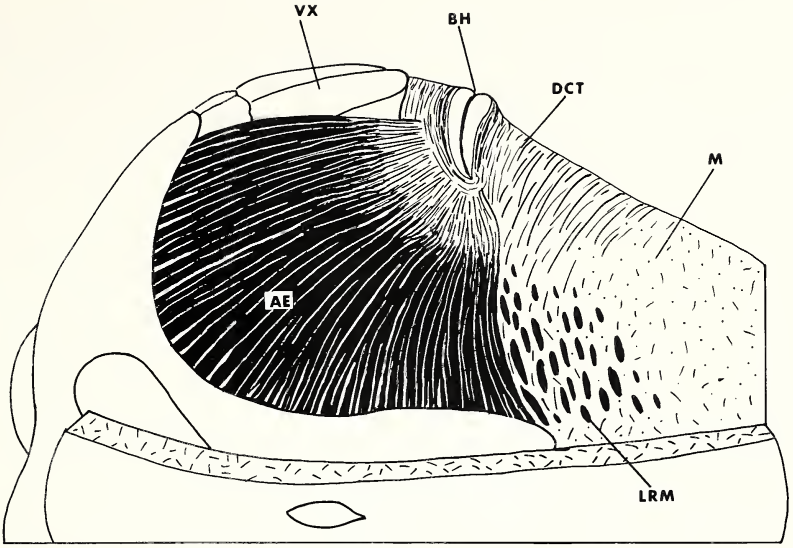


**Figure 22.** Right lateral view of the region of the facial fossa of *Ziphius cavirostris* (HSUZ 4471) with the blubber layer and superficial fascia removed. AE = pars anteroexternus, BH = blowhole, DCT = dense connective tissue, LRM = lateral rostral muscle, M = melon, VX = vertex.

surrounding the blowhole. These fibers form a small intrinsic muscle of the blowhole. However, this muscle is so small that it cannot function as the sole closing mechanism of the distal respiratory system.

The rostral muscles originate on the rostrum from approximately 15 cm behind the rostral tip posteriorly to the antorbital region, where the fibers merge with the pars anterointernus. Anteriorly on the rostrum, numerous muscle bundles originate from the lateral edges of the maxillae and radiate laterally, with fibers extending both ventrally into the tissue around the angle of the mouth, and dorsally and medially onto the melon. Posteriorly, the lateral rostral muscle has fewer fibers inserting onto the region posterior to the gape; the majority of the muscle inserts onto the melon or the dense connective tissue mat that is situated dorsal to the melon posterior to the antorbital notches. Approximately at midrostrum is a connective tissue band that divides the rostral muscle into lateral and medial components. Posteriorly, the fibers of the lateral rostral muscle insert directly onto the blubber lateral to the melon at the antorbital region.

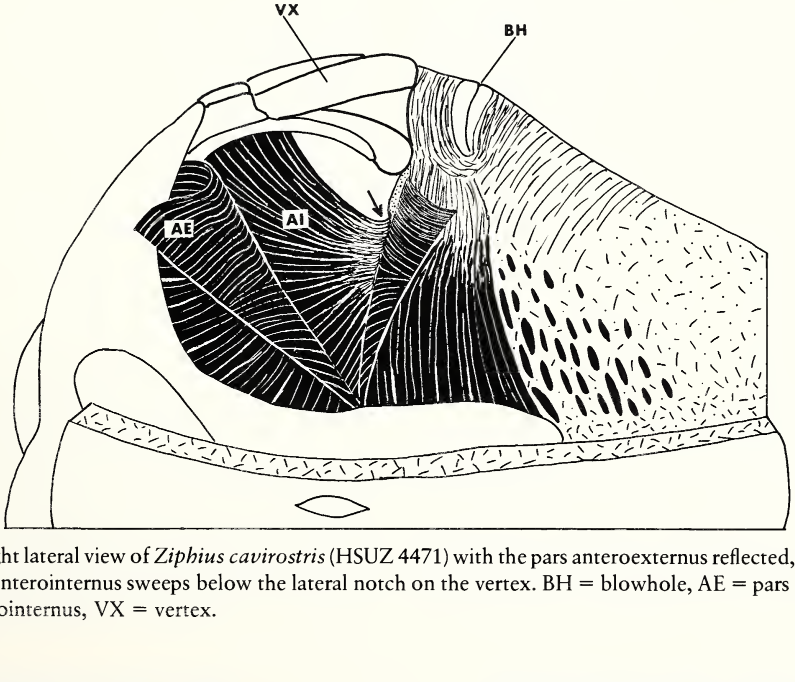


**Figure 23.** Right lateral view of *Ziphius cavirostris* (HSUZ 4471) with the pars anteroexternus reflected, arrow indicates where the pars anterointernus sweeps below the lateral notch on the vertex. BH = blowhole, AE = pars anteroexternus, AI = pars anterointernus, VX = vertex.

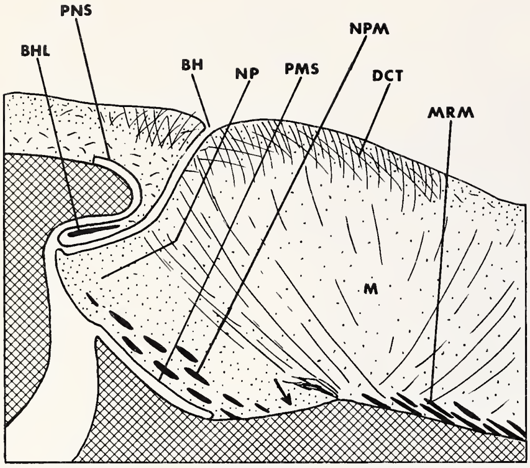


**Figure 24.** Diagrammatic parasagittal section through the right naris of a subadult male *Ziphius cavirostris* (USNM 550803). Note the incipient prenarial basin (arrow). BH = blowhole, BHL = blowhole ligament, DCT = dense connective tissue, M = melon, MRM = medial rostral muscle, NP = nasal plug, NPM = nasal plug muscle, PMS = premaxillary sac, PNS = posterior nasal sac.

The melon is fairly typical in construction for odontocetes (Figs. 22, 24). Anteriorly on the rostrum, it consists of adipose tissue within moderately dense connective tissue. Approximately 20 cm posterior to the rostrum tip the melon contains less connective tissue and is well differentiated into an outer melon with some long collagen fibers and the inner melon, or core, that virtually lacks connective tissue fibers. The inner melon or core is situated just dorsal to the premaxillae in a medial position. At the antorbital region, the melon core expands considerably to occupy almost the entire melon region in this area. At the level of the blowhole, the melon becomes smaller, restricted to the center of the facial region, and set slightly to the right side. The decrease in the size of the melon in this region is related to the increase of the medial rostral muscle. Dorsal to the melon in this section is a dense mat of intertwining connective tissue fibers oriented concentrically over the melon (Fig. 22). As in most odontocetes, the core of the melon extends posteriorly into the right nasal plug but not into the left. In a parasagittal section of the melon (Fig. 24), the connective tissue fibers radiate anterodorsally, anteriorly, and posterodorsally along the posterior third of the melon. In transverse sections of the rostrum, these fibers form crescent-shaped bands over the rostrum.

The blowhole ligaments are tautly drawn against the spiracular surface of the vertex (Fig. 21). Because the spiracular surface of the right premaxilla is several times as wide as the left, the anatomical median at the mesethmoid is displaced far to the left side of the facial region. The blowhole ligaments extend from the junction of the mesethmoid and the nasals to the lateral edges of the premaxillae. The left blowhole ligament is therefore oriented almost vertically, whereas the right blowhole ligament is inclined at approximately 45° ventrolaterally. The right blowhole ligament is thus considerably longer than the left. Within the leading edge of the left blowhole ligament is a section of hyaline cartilage that gives the leading edge of the ligament rigidity.

Correlated with the marked asymmetry of the skull, the right nasal plug is about two to three times as wide as the left. The rounded posterior surface fits tightly against the entire spiracular surface of the vertex. There are distinct creases on the posterior surfaces of the nasal plugs that correspond with the folds formed by the blowhole ligaments on the adjacent spiracular surface of the vertex. At the anterior end of the spiracular plate on the right premaxilla is a small ridge of connective tissue.

The nasal plug muscles are also quite asymmetrical in size. The larger right muscle originates on the premaxilla just anterior and lateral to the right premaxillary sac. The left nasal plug muscle is much smaller and originates only lateral to the left premaxillary sac. In the bony trough on the dorsal aspect of the skull at the premaxilla/maxilla suture is another muscle whose fibers are directed posterodorsally onto the ventral aspect of the core of the melon. This medial muscle of the rostrum becomes smaller and more diffuse posteriorly at approximately the level of the antorbital notches, but appears to grade into the nasal plug muscle.

## Adult Male

**Nasal passages.** In addition to the formation of the prenarial basin, the skulls in adult males also widen at, and develop a deeper concavity to, the spiracular surface of the vertex (Fig. 25). Accordingly, the nasal vestibule is wider distally in males than in females. Most of this lateral enlargement is related to the enlargement of the right nasal plug.

The right posterior nasal sac is similar to that found in females with the exception that the connective tissue in the vertex cleft has one or two slight transverse lunate ridges on its surface. On the left side, the posterior nasal sac is present, but considerably smaller than the right sac. It is situated primarily lateral to the blowhole ligament and is shaped as a small rounded pocket approximately 2 cm in diameter.

The right premaxillary sac is a wide flattened funnel-shaped diverticulum (Fig. 25). It extends broadly anteriorly and ventrally along the bony surface of the prenarial basin for several cm and then tapers to a narrow tube that extends medially into the soft tissue of the prenarial basin approximately 16 cm in front of the bony nares. The narrow distal end is just lateral to the medial septum, medial to the right nasal plug muscle, and dorsal to the fatty contents of the prenarial basin. This anterior extension of the right premaxillary sac is unique in

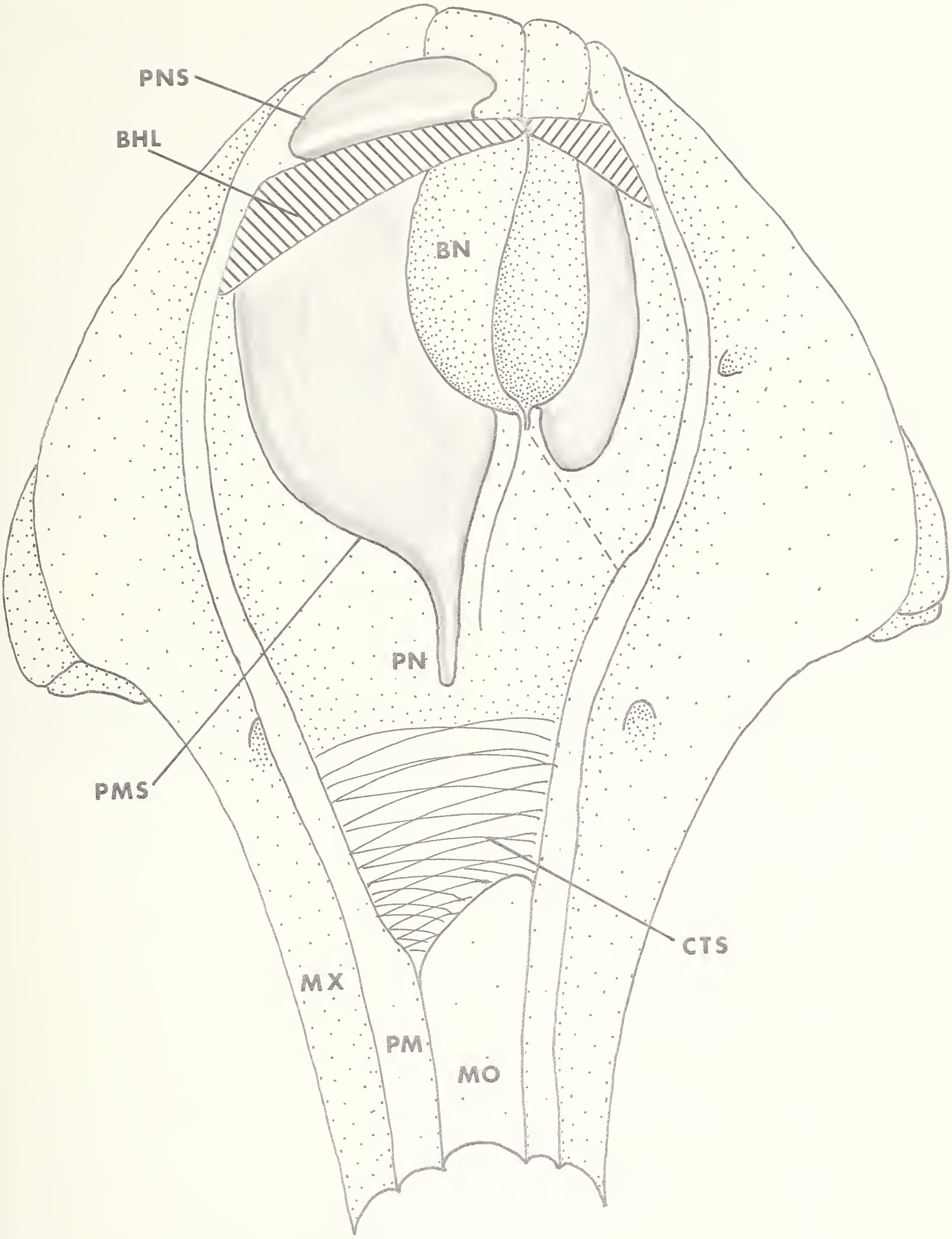


**Figure 25.** Anterodorsal view of an adult male *Ziphius cavirostris* illustrating the nasal diverticula, bowhole ligaments, and prenarial basin. All of the left and most of the right posterior nasal sacs are covered in this view by the blowhole ligaments (hatched region). Dashed line indicates the position of the medial septum that divides the right and left nasal plugs. BHL = blowhole ligament, BN = bony naris, CTS = connective tissue sheath, MO = mesorostral ossification, MX = maxilla, PM = premaxilla, and PMS = premaxillary sac, PN = prenarial basin, PNS = posterior nasal sac.

that it is not in contact with the bony surface of the premaxilla. The left premaxillary sac is similar to the same structure found in females and young males.

**Soft Anatomy.** Other than the nasal plug muscles, the facial musculature is quite similar to that found in females and young males.

The greatest asymmetry in the facial anatomy of

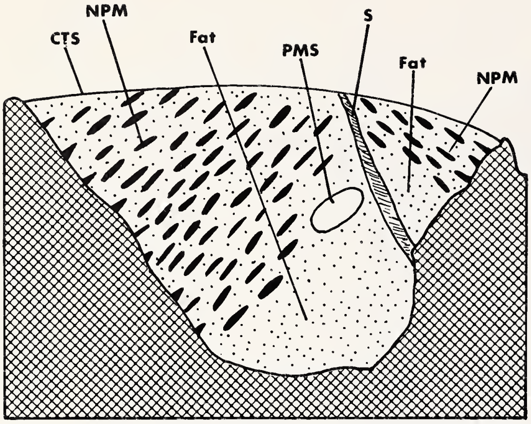


**Figure 26.** Anterior view of a diagrammatic cross section through the prenarial basin of *Ziphius cavirostris* (HSUZ 4471) at the level of the antorbital region. Note the extreme asymmetry in that the medial septum is displaced distinctly to the left, and that only the right premaxillary sac extends this far anteriorly. CTS = connective tissue sheath, NPM = nasal plug muscle, PMS = premaxillary sac, S = septum.

a mature male *Ziphius* is in the paired nasal plugs. The median septum that divides the two halves runs at an angle from the mesethmoid at the anterior edge of the bony nares to a bony prominence situated on the left premaxilla several cm forward on the lip of the prenarial basin. Thus, the geometrically medial prenarial basin is essentially filled with the right nasal plug. The tissue within the posterior part of the right nasal plug is similar to that in most odontocetes in that the fatty tissue of the melon extends quite far posteriorly into the right plug. The anterior region of the prenarial basin is unique among odontocetes in that it becomes filled with fat that has progressively fewer connective tissue fibers running through it (Figs. 25, 26). At the most anterior section of the basin the tissue is essentially pure white fat or a clear viscous oil. On the floor of the prenarial basin adjacent to the medial septum is a small dense blood vessel network. The bony floor of the prenarial basin has a very rugose texture. In life, however, the floor is covered with connective tissue that gives it a relatively smooth surface. The contents of the prenarial basin in this region are covered with a thin but dense connective tissue sheath that originates from the dorsal anterior rim of the premaxillae bounding the basin (Figs. 24, 26). This structure is what Norris and Harvey (1972) described as "a small subcylindrical fatty organ, that may be homologous to the spermaceti organ, occupied an excavation in the surface of the rostrum and communicated posteriorly to the right nasal plug that was lined on its surface by a morticebordered museau." Several cm posterior to the anterior edge, the fibers within this sheath become more diffuse, and the tissue below also has more fibers running through it and hence greater integrity. In subadult males and mature females, there is a small connective tissue covering less than 2 cm long over the anterior aspect of the spiracular plate on the right premaxilla. The left nasal plug is much smaller and consists primarily of connective tissue with some interspersed adipose tissue. The posterior surface of the nasal plugs is relatively enlarged. This enlargement is presumably related to the increased size of the spiracular surface of the vertex caused by the prenarial basining. The nasal plugs lack lateral lips.

The paired nasal plug muscles are asymmetrical in size, corresponding with the extreme enlargement of the right nasal plug. The fibers of these muscles are in loosely arranged bundles within a fatty matrix and originate from the respective lateral walls of the prenarial basin. The origin of the right nasal plug muscle extends lateral to the corresponding premaxillary sac from the level of the bony nares anteriorly to approximately midlength of the prenarial basin. The left nasal plug muscle has a more restricted origin from a small area just anterior and lateral to the premaxillary sac.

### *Berardius bairdii*

The facial anatomy of *Berardius* spp. is of interest because the facial region of the skull is the most primitive among living ziphiids in lacking a highly elevated cranial vertex (Moore, 1968). The facial region of the skull is also less asymmetrical than other extant ziphiids. In these respects, the facial region of *Berardius* spp. resembles platanistids, iniids, and delphinoids. Barnes (1978) noted that the vertex region of *Berardius* spp. resembles the primitive delphinoid *Lophocetus repenningi*. As with most odontocetes, the facial soft anatomy is more asymmetrical than the underlying cranial features.

The only published description of the facial anatomy of *Berardius bairdii* is a diagram of the nasal passages and diverticula figured by Yablokov et al. (1974). The sketch they present is so crude however that no details can be ascertained from it and there is no accompanying text. The general pattern appears to be similar to other ziphiids and includes the anterior aspects of the nasofrontal sacs.

The following description is based on the dissection of a subadult animal and a near-term fetus. The general facial anatomy of these two animals was quite similar, but differed considerably in some details from Yablokov et al.'s (1974) illustration.

**Nasal Passages.** The blowhole in *Berardius* is unique in that it is a wide shallow crescent with apices that are directed posteriorly (Fig. 27) rather than anteriorly, as in most odontocetes. The nasal vestibule extends ventrally in a nearly vertical plane, tilting posteriorly about 20° (Fig. 29). The vestibule widens only slightly deep to the blowhole. There is no vestibular sac nor any folds or creases on the surface of the vestibule.

The sacs posterior to the blowhole ligaments are partially divided into two parallel sacs by large transverse fleshy folds similar to those seen in pho-

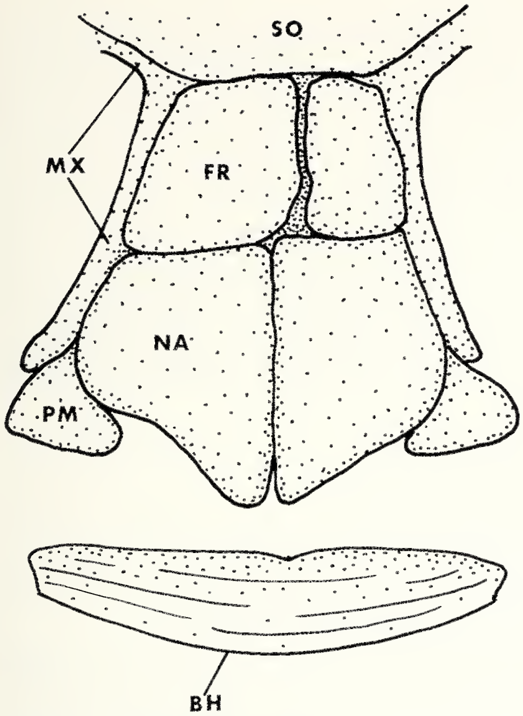


Figure 27. Diagrammatic dorsal view of the nasal vestibule of *Berardius bairdii.* BH = blowhole, FR = frontal bone, MX = maxilla, NA = nasal, PM = premaxilla, SO = supraoccipital, V = vestibule.

coenids (Fig. 29). The more anterior sac, the posterior portion of the nasofrontal sac, appears to be more distensible dorsally and both appear to be quite distensible along their lateral margins as judged by the crenulated epithelium found in these regions. The more caudal posterior nasal sac is considerably smaller in both specimens that I dissected (Fig. 28).

There are no anterior sections to the nasofrontal sacs. The illustration presented by Yablokov et al. (1974) indicates that the anterior sections are present in *Berardius bairdii,* however the drawing of the skull looks more like a *Ziphius cavirostris* than that of *Berardius* spp., and the detail is quite crude. In light of the fact that facial soft anatomy appears to be rather conservative within other species of odontocetes, it seems unlikely that some specimens of *Berardius* lack the anterior sections of the nasofrontal sacs, whereas in other specimens these structures are well developed.

The premaxillary sacs are approximately equal in size, but otherwise typical in shape and location for most odontocetes. The only difference is that a small portion of both sacs extends along the lateral edge of the premaxillae in the region of the lateral attachment of the blowhole ligament. This section of the premaxillary sacs is not appressed by the blowhole ligament and therefore might be a region by which air can be passed around the blowhole ligaments.

**Soft Anatomy.** The external robustness of *Berardius* is due primarily to the thick blubber layer that is approximately 10 cm thick at the posterior region of the cranium. The connective tissue within the blubber becomes more dense anterior to the level of the blowhole. It is most extensive just anterior to the blowhole on the dorsal surface.

The facial musculature is relatively smaller in mass than in other ziphiids correlated with the shallowness of the facial fossa. The pars anteroexternus originates along the entire facial border much as in other ziphiids. However, due to the low elevation of the vertex, the anterior fibers that originate from

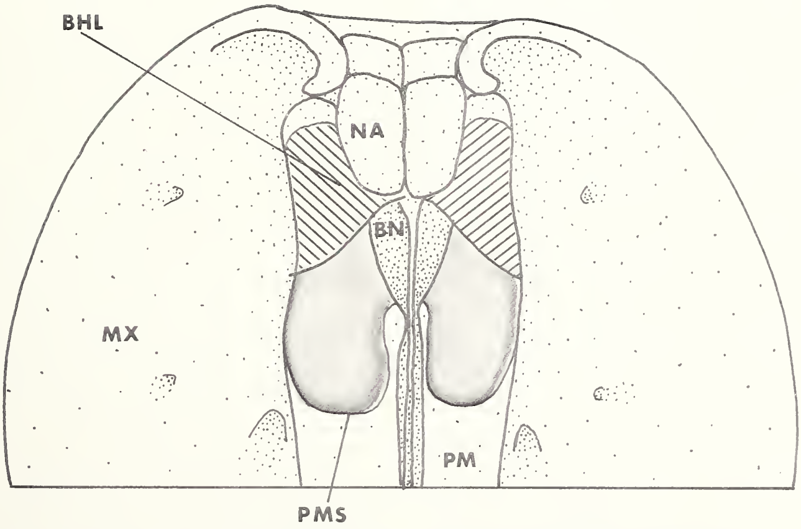


Figure 28. Anterodorsal view of the nasal diverticula of *Berardius bairdii.* The hatched region represents the approximate position of the blowhole ligaments behind which lie the paired posterior portion of th nasofrontal sacs and the posterior nasal sacs. BHL = blowhole ligament, BN = bony naris, MX = maxilla, PM = premaxilla, PMS = premaxillary sac.

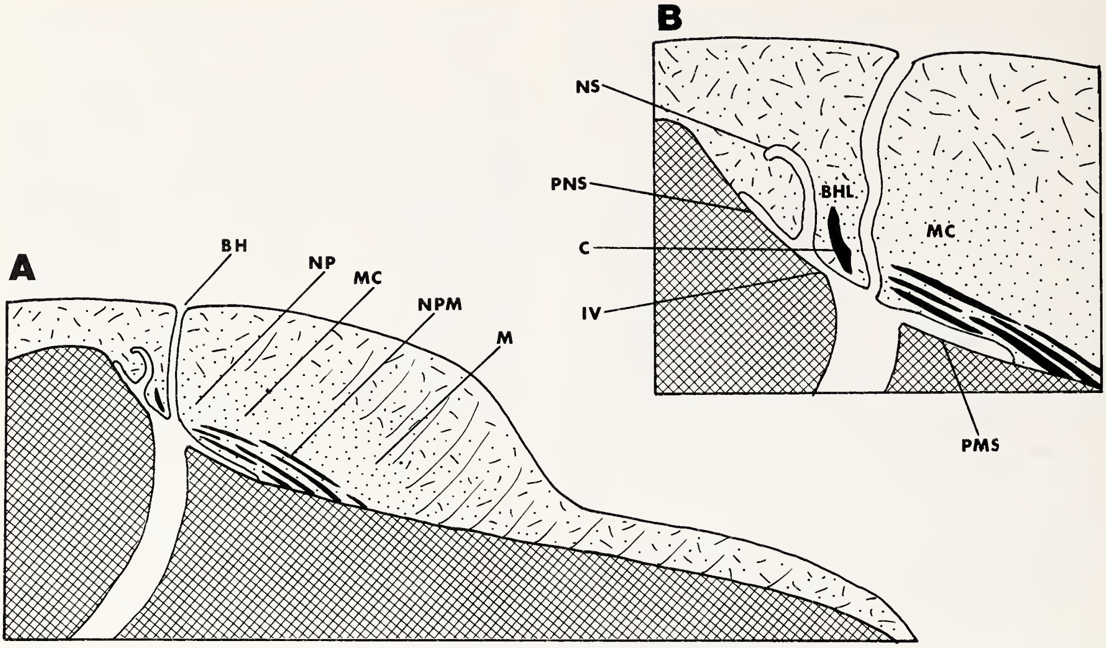


**Figure 29.** **A,** Diagrammatic parasagittal section through the right naris of *Berardius bairdii.* **B,** Enlargement of narial region. BHL = blowhole ligament, BH = blowhole, C = cartilage, IV = inferior vestibule, M = melon, MC = melon core, NP = nasal plug, NPM = nasal plug muscle, NS = nasofrontal sac, PMS = premaxillary sac, PNS = posterior nasal sac.

the antorbital region extend posteriorly at a more longitudinal angle than in other ziphiid species that I have dissected. The pars anteroexternus is relatively thick for ziphiids. In the subadult animal that I dissected, it measured approximately 3 cm thick posteriorly in the facial fossa and 2 cm thick more anteriorly. The pars anteroexternus and pars anterointernus were not well differentiated because the fibers ran approximately parallel in most regions. These two muscles were almost inseparable in the anterior section of the facial fossa.

In the subadult specimen, the rostral muscle began approximately 25 cm posterior to the tip of the rostrum. Along the beak, the rostral muscle remains small, and about at the region where the head widens (45 cm from the rostral tip) it can be differentiated into fibers that are oriented posterodorsally and posterolaterally. Immediately dorsal to the rostrum in this region are loosely arranged transversely oriented muscle fibers. In sagittal section, these muscle fibers are oriented in an anterodorsal direction and are limited to the anterior portion of the melon. Approximately 60 cm posterior to the rostral tip, the rostral muscles become quite extensive, originating broadly along the dorsal aspect of the maxillae and inserting onto the ventral and lateral surface of the melon. Posterior to this, the rostral muscle grades into the pars anterointernus.

The "beak" region consists of fatty blubber with relatively small amounts of connective tissue fibers in it. A more defined melon does not begin posteriorly until the region where the facial soft anatomy abruptly expands dorsally. This large squared-off "forehead" or melon region typical of this species is formed primarily of the thickened blubber and connective tissue layer dorsal to the melon (Fig. 29). The melon appears to be typical in gross morphology for ziphiids, but is relatively smaller than the melons of other ziphiid species that I have dissected. It appears in transverse section as a dorsoventrally compressed ovoid that is situated primarily dorsal to the premaxillae. It is obviously asymmetrical in that it is larger on the right side anteriorly, and, at the level of the blowhole, it is situated entirely on the anatomical right side of the animal. The melon extends posteriorly to the back end of the right nasal plug and thus is similar in this feature to most odontocetes.

The blowhole ligaments are considerably more fleshy than those found in other ziphiids (Fig. 29). This is because, although the nasal vestibule is oriented in a nearly vertical plane, the vertex of the skull is not very elevated and thus there is a great deal of space between the vestibule and the vertex of the skull. From an anterior view, the blowhole ligaments extend from the dorsolateral aspect of the bony nares and run at about a 45° angle ventrolaterally to the lateral edge of the premaxillae. The right blowhole ligament is slightly larger than the left, but not nearly as asymmetrical as these structures are in other species of ziphiids. The blowhole ligament has a section of hyaline cartilage embedded within a thick mass of softer connective and adipose tissue. This adipose tissue is slightly more pronounced anterior to the cartilage.

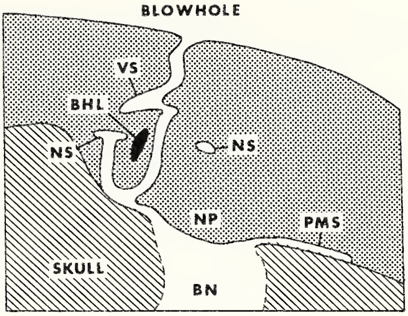
The nasal plugs are similar in morphology to those of most other odontocetes. The fatty melon core extends posteriorly in the right nasal plug to the surface that is adjacent to the blowhole ligaments (Fig. 29). The left nasal plug is filled primarily with the relatively larger left nasal plug muscle. However, there is a small amount of isolated adipose tissue along the posterior surface of the left nasal plug. Both the right and left nasal plugs of *Berardius bairdii* are unique among the ziphiid species examined in that they have fairly well-formed lateral lips to the nasal plugs similar to those seen in delphinoids. The paired nasal plug muscles originate from the premaxillae and along the dorsal surface of the premaxillary sacs.

### *Tasmacetus shepherdi*

Due to the rarity of strandings of *Tasmacetus shepherdi,* I was not able to obtain a specimen to dissect and there are no published accounts describing the facial anatomy of this monotypic genus. J.G. Mead kindly provided his unpublished notes on his dissection of a 660-cm female (USNM 484878). Other details on this specimen have been published elsewhere (Mead and Payne, 1975).

**Nasal Passages.** The blowhole is an assymmetrically oriented deep crescent with apices that are directed anteriorly. The right apex extends much farther anterior than the left apex. The vestibule of the distal nasal passage extends in an almost vertical plane ventrally to just in front of the vertex of the skull. The vestibule widens laterally slightly as it extends downward. This transverse widening extends approximately twice as far on the right side as on the left. The blowhole ligaments are large. Passing from beneath these ligaments and extending dorsally are a series of paired nasal sacs. The inferior vestibules and posterior aspect of the nasofrontal sacs are quite large, and there is no clear differentiation between the two sacs as seen in delphinoids. This appears to be similar to what is seen in other ziphiids. It is unclear from the description whether there are well-formed posterior nasal sacs and posterior nasofrontal sacs or whether one of these sacs has been reduced as is the case with *Ziphius* and *Mesoplodon.* The accessory sacs are small, only 1–1.5 cm in diameter, and extend slightly laterally approximately 1.5 cm as small outpockets. The premaxillary sacs are relatively small, with the right sac larger than the left.

**Soft Anatomy.** There was no indication of either a pars posteroexternus or pars intermedius muscle. The pars anteroexternus is quite large. The pars anterointernus is well developed. Its posterior fibers originate from the facial fossa and insert on the anterior surface of the posterior nasal sacs. On the anterior aspect of these sacs, the paired insertions of the posterior fibers of the pars anterointernus interweave medially, forming a transverse band of muscles. The nasal plug muscle is long but not particularly large, corresponding with the small size of the nasal plugs. In cross section, the well-developed rostral muscles could be differentiated into both lateral and medial components.



DELPHINID

**Figure 30.** Diagrammatic parasagittal section through the right naris of a typical delphinid, to illustrate the airways. The anterior section of the nasofrontal sac appears as a hole in this section. BHL = blowhole ligament, BN = bony naris, NP = nasal plug, NS = nasofrontal sac, PMS = premaxillary sac, VS = vestibular sac.

The connective tissue surrounding the anterior and posterior aspects of the blowhole was quite dense. The hypodermis is apparent firmly attached to the vertex of the skull with connective tissue. The fattiest region of the melon proper is relatively small compared to that in other odontocetes of this size. The melon region consisted primarily of connective tissue bundles in a fatty matrix. The nasal plugs were also relatively small and lacked lateral lips. There were no diagonal membranes reported for this specimen.

## SYSTEMATIC REVIEW OF ODONTOCETE FACIAL ANATOMY

In the following section, the salient features of each odontocete family are summarized and deviations from this generalized model are noted. This provides the groundwork for a comparative analysis and for a systematic review. The following descriptions are drawn primarily from Mead (1975a) and Schenkkan (1973), with contributions from other works as cited and my dissections of the various species.

### FAMILY DELPHINIDAE

Although the family Delphinidae is the most species-rich and exhibits extensive variation in external morphologies, the pattern of the facial anatomy is quite conservative (Fig. 30). The vestibular sac is a simple undivided horizontally flattened sac that typically extends posterolaterally from the unpaired nasal passage. Its surface is often wrinkled in appearance, illustrating that it is distensible in life, but never heavily folded. Schenkkan (1973) reported that the vestibular sac of *Lagenorhynchus obliquidens* extends quite far rostrally, which is not the condition in other delphinids including the congeneric species examined, *L. albirostris, L. obscu-*

*rus,* and *L. acutus* (Schenkkan, 1973; Mead, 1975a). My findings, based on dissections of three *L. obliquidens,* concur with those of Schenkkan although the left half of the vestibular sac extended much farther anteriorly than the right. Schenkkan (1973) noted that his specimen was damaged on the right side, and thus he extrapolated from the more intact left side. If this feature is consistent and unique to *L. obliquidens,* then the idea that this species is only the northern form of *L. obscurus* (Honacki et al., 1982) would seem to be incorrect.

The nasofrontal sac is the most varied of the nasal diverticula. The anterior aspect of the sac is slightly enlarged in *L. albirostris* and greatly enlarged in *Cephalorhynchus hectori* (Schenkkan, 1973; Mead, 1975a). I also have found that the anterior portions of the nasofrontal sacs are greatly enlarged in *Cephalorhynchus commersoni.* The entire left anterior component of the nasofrontal sac is lacking in specimens of *Grampus griseus* dissected by Murie (1870), Mead (1975a), and myself. Mead (1975a) also described a unique trabeculated sacculation on the angle of the right nasofrontal sac in *Globicephala melas* (= *G. melaena*). The accessory sacs of delphinids are always small and conservative in shape and position.

The premaxillary sacs are usually the largest sacs within the facial region of delphinids and are also consistent in shape and size. The right one is always larger than the left, but typically is much wider, extending anteriorly only slightly farther than the left sac.

The two superficial muscles, the pars posteroexternus and the pars intermedius, are the most variable as to size and even presence. The deeper muscles are extremely conservative; however, they are often difficult to differentiate completely from one another.

Most of the smaller dolphin species have relatively small melons. *Globicephala* spp., *Grampus griseus,* and *Pseudorca crassidens* have hypertrophied melons, which is reflected in their external bulbous appearance. Mead (1975a) reported that the melon always extends posteriorly into the right nasal plug, except in *P. crassidens* and *Cephalorhynchus hectori.* In my dissections of two *C. commersoni,* I found that the melon does not protrude into either nasal plug. However, the melon did extend into the right nasal plug of the adult *P. crassidens* that I dissected. The significance of this lack of melon in the right nasal plug in at least some specimens of these two dissimilar genera is unknown and the feature is probably due to parallel evolution.

## FAMILY PHOCOENIDAE

The facial anatomy of phocoenids has been described for *Neophocaena phocaenoides* by Howell (1927), for *Phocoena phocoena* by Moris (1969), Schenkkan (1973), and Mead (1975a, and literature cited therein), and for *Phocoenoides dalli* by Mead (1975a). Knowledge of *Phocoena phocoena* and *Phocoenoides dalli* was supplemented by my own dissections.

The vestibular sacs in phocoenids (Fig. 38) are quite different from those found in delphinids and are relatively twice as large. They extend primarily anterolaterally from the nasal passage, with a smaller portion extending posteriorly. The aperture of the vestibular sacs is a single medial opening to the anterior aspect of the nasal passage approximately 1 cm deep to the blowhole in the specimens of *Phocoena phocoena* that I dissected. The bilaterally paired sacs become divided immediately anterior to this aperture. This total bilateral division of the vestibular sacs appears to be consistent throughout the family. The dorsal surfaces of the sacs are slightly wrinkled as in delphinids, but the floor has several deep transverse folds in it. The floor also has sufficient dense connective tissue in it to be fairly rigid. Although these folds are described as being transverse in orientation, I found them to be somewhat concentrically oriented anterior and posterior to a straight medial transverse fold (see Schenkkan, 1973: 148).

The nasofrontal sac of phocoenids was described by Howell (1927), Schenkkan (1973), and Mead (1975a). These sacs are proportionately larger than those found in delphinids. There is a small dorsal expansion of the posterior nasofrontal sac reported for *Phocoena phocoena,* but its details have not been described (Mead, 1975a). The sacs posterior to the blowhole ligament are transversely divided by a fleshy fold of tissue extending downward into the sac (Fig. 38). The divisions of the sac are confluent along the ventral border of this fold and around its medial border. Moris (1969) named the more caudal sac the posterior nasal sac, and I have used the term posterior nasofrontal sac for the more cranial diverticula (see Homology section). This structural arrangement is also found in monodontids, *Inia, Platanista, Berardius,* and *Hyperoodon,* and I have used this terminology consistently.

One of the major cranial features unique to phocoenids is the presence of small bony bosses, or eminences, on the spiracular plate of the premaxillae. The small premaxillary sacs sit upon the slightly rugose surfaces of these bosses. Thus, Fordyce's (1981) term of "premaxillary sac fossa" for the spiracular plate is somewhat inappropriate because this smooth "fossa," indicating the approximate limits of the premaxillary sac in delphinids and ziphiids, is not evident in monodontids and phocoenids even though these groups also possess premaxillary sacs. Therefore, the lack of a distinct smooth spiracular plate cannot be used as evidence for the lack of premaxillary sacs in fossil odontocetes.

Detailed descriptions of the facial musculature have not been published. The general pattern is that the pars posteroexternus appears to be absent in phocoenids, but the deeper muscles are similar to what is found in delphinids. However, phocoenids have a unique intrinsic muscle surrounding the vestibular sac (Schenkkan, 1973); this muscle is not found in other delphinoids (Mead, 1975a).

The melon is described as being similar to that in delphinids. I found the melon in *P. phocoena* to be a relatively small and more discrete structure than that found in delphinids or ziphiids; it did not extend posteriorly into either nasal plug. In regard to the small nasal plugs and the reduced discrete melon that does not project into either nasal plug, phocoenids are similar to the anatomically described species of the delphinid genus *Cephalorhynchus.* It is interesting to note that similarities in phonations between *Phocoena* and *Cephalorhynchus* were discussed by Watkins et al. (1977). Both of these genera have enlarged nasal diverticula dorsal to the melon. In *Cephalorhynchus,* it is the anterior section of the nasofrontal sacs and in phocoenids it is the hypertrophied vestibular sacs. The blowhole ligaments are angled in a similar orientation to the ligaments in ziphiids (Schenkkan, 1973).

## FAMILY MONODONTIDAE

Many features of the facial anatomy of monodontids have not been described in sufficient detail to allow a thorough comparative statement. There is even some question in the literature as to whether or not these two genera are very closely related (Kasuya, 1973). It is clear that more research is needed on monodontid anatomy and systematics. However, the published illustrations of the nasal diverticula of both species are quite similar (Huber, 1934; Kleinenberg et al., 1969). Thus, I assume that these two monotypic genera are monophyletic and limit my discussion to *Delphinapterus leucas,* the species better described in the literature and for which I was able to dissect a moderately preserved specimen. The facial region of the skull is unique among odontocetes in that the entire surface is slightly convex rather than concave. The spiracular plate also differs from those in delphinids and ziphiids in that it is slightly rugose.

Kleinenberg et al. (1969) described the vestibular, premaxillary, and nasofrontal sacs as being similar, in general, to the pattern found in delphinids, but they did report on a small posterodorsal extension of the posterior nasofrontal sacs (e.g. the posterior nasal sacs) similar to that in *Phocoena phocoena.* My dissection concurs that the premaxillary sacs and the anterior section of the nasofrontal sacs are similar to delphinids. The vestibular sac is separated into a right and left side with apertures on the anterior aspect of the vestibule. In this feature, the vestibular sac is similar to that structure found in phocoenids. Posterior to the blowhole ligament, the inferior vestibule divides dorsally into a rostral nasofrontal sac and caudally into a posterior nasal sac.

The melons of both *D. leucas* and *M. monoceros* are quite large. In *D. leucas,* is is slightly flaccid, and the muscular control of it can be seen externally during phonation (Norris and Harvey, 1974). I found the rostral muscle in *D. leucas* to be relatively larger than that in other species of odontocetes that I have dissected. The melon extends posteriorly into the right nasal plug and to a lesser degree into the left nasal plug. I noted a small piece of cartilage in the blowhole ligament of the specimen that I dissected.

### "Superfamily Platanistoidea"

The systematics of this taxon is currently in a state of confusion, with widely differing classifications in the literature. The four extant genera in this taxon are variously placed within one family (Platanistidae), or in three or four separate families within the superfamily Platanistoidea. Most of the recent systematic works have dealt with emphasizing the degree of differences between species but have not addressed directly the systematic question of whether the group is monophyletic or not.

Based on my analysis (see Systematics section) using a wide range of morphological characters, the Platanistoidea appears to be a paraphyletic grouping. According to my analysis, there are two monophyletic groups: the Iniidae including the extant genera *Inia, Lipotes,* and *Pontoporia;* and the Platanistidae including only *Platanista.*

## FAMILY PLATANISTIDAE

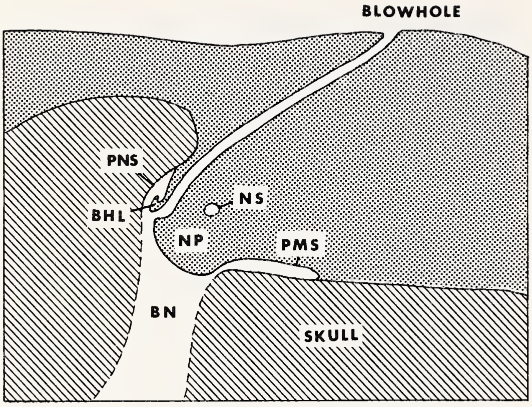
No specimens of any *Platanista* spp. were available to me. The following account is based on Anderson (1878) and Purves and Pilleri (1973).

The blowhole of *Platanista* is unique in being a longitudinal slit. *Platanista* lacks a vestibular sac and the distal nasal vestibule is a laterally flattened tube that is oriented in a posteroventral plane (Anderson, 1878:451). It is clear from the illustrations and descriptions of Purves and Pilleri (1973) that the nasal diverticula posterior to the blowhole ligaments are quite complex. The more caudal portion of this complex that extends dorsally along its medial border is interpreted here as homologous with the posterior nasal sac of other odontocetes. The more rostral nasofrontal sacs of *Platanista* are described as being similar to the nasofrontal sacs of delphinids except that the anterior aspects are directed dorsally instead of anteriorly (Purves and Pilleri, 1973). *Platanista* is reported to have relatively small premaxillary sacs.

River dolphins of the genus *Platanista* have unique maxillary crests that overhang the facial region anteriorly. The ventral surfaces of these crests are covered by a thin flat complicated air sac derived from the pterygoid air sinus system that forms part of the ventral air sac system of the skull (Fraser and Purves, 1960; Purves and Pilleri, 1973). This is clearly a highly derived feature of the facial anatomy.

## FAMILY INIIDAE

The following summary of the facial anatomy of iniids is taken from Schenkkan (1972) and Mead (1975a) for *Pontoporia blainvillei,* Mead (1975a)



MESOPLODON

**Figure 31.** Diagrammatic parasagittal section through the right naris of a typical *Mesoplodon* sp. to illustrate the airways. The anterior aspect of the nasofrontal sac (not present in *M. densirostris*) appears as a hole in this section. BHL = blowhole ligament, BN = bony naris, NP = nasal plug, NS = nasofrontal sac, PMS = premaxillary sac, PNS = posterior nasal sac.

and Schenkkan (1977) for *Inia geoffensis,* and from Hinton (1936) and Chen et al. (1980) for *Lipotes vexillifer.* In addition, I was able to dissect one specimen each of *I. geoffrensis* and *P. blainvillei.*

The blowholes in *Inia* and *Pontoporia* are transverse crescents very similar in shape to the blowhole of delphinoids. Hinton (1936) described the blowhole in *Lipotes* as longitudinal and somewhat rectangular. Hinton (1936) also described what appeared to be small "bones" on either side of the blowhole. Chen et al. (1980) found that these bones were actually compact masses of connective tissue.

The vestibular sac is greatly enlarged, especially on the right side, and is somewhat variable in detail among iniids. The right side of the vestibular sac of iniids extends anteriorly, posteriorly, and lateroventrally covering almost the entire muscle mass of the facial fossa on the right side. In *Inia,* Schenkkan (1977) noted an anterior connection between the right and left sides of the vestibular sacs, but Mead (1975a) did not mention this. The left side of the vestibular sacs is much smaller than the right in *Pontoporia* and *Lipotes,* and moderately enlarged in *Inia.*

In *Pontoporia* and *Inia,* the anterior aspects of the nasofrontal sacs are lacking and the posterior portions are reduced in size (Mead, 1975a). In the specimen of *Pontoporia* that I dissected, the nasofrontal sac extended anteriorly about 1 cm, at least on the right side. Schenkkan (1977) reported that the nasal sacs posterior to the blowhole ligament are divided by a transverse fleshy fold, similar to the condition found in *Phocoena phocoena.* The nasal sacs posterior to the blowhole ligament of *Lipotes* have not been described in detail, but no anterior portions of the nasofrontal sacs are present. The accessory sacs are reported to be lacking in *Pontoporia* and *Lipotes,* but are well developed in *Inia* and similar in shape to the accessory sacs of delphinids. I found the accessory sacs to be moderately developed in the *Pontoporia* that I examined.

Both *Inia* and *Pontoporia* are described as having premaxillary sacs similar in size and shape to those found in delphinoids. The right premaxillary sac of *Lipotes* is described as being slightly larger than the left and appears to be relatively small in size compared to delphinids.

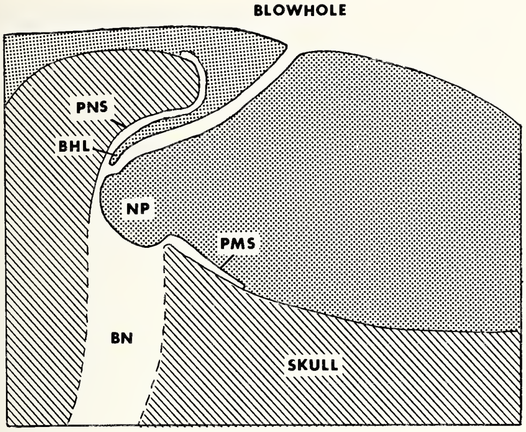
The melons of *Inia* and *Pontoporia* are reported to be similar to the melon of delphinids except that they have relatively more connective tissue. The nasal plugs of these species are described as similar to delphinids, but lacking lateral lips (Mead, 1975a).

## FAMILY ZIPHIIDAE

### Nasal Passages

The blowhole in ziphiids is a shallow to deep crescent-shaped transverse slit. The apices of the crescent are directed forward in all known species except those of the genus *Berardius,* in which the apices are directed posteriorly. The nasal passage is an anteroposteriorly flattened tube when relaxed, and there is no vestibular sac. In species of those genera in which the vertex is greatly enlarged (*Hyperoodon, Mesoplodon,* and *Ziphius*), the distal nasal passage slants posteriorly from the blowhole to the bony nares (Figs. 31–33). In *Tasmacetus shepherdi* and *Berardius* spp. the vertex of the skull is not highly elevated, and the distal nasal passage is oriented in a nearly vertical plane, as is the case also for delphinoids and iniids. As the nasal passage approaches the vertex of the skull, it widens laterally and typically extends slightly beyond the lateral edge of the premaxillae on the vertex.

Extending first posteriorly and then dorsally from behind the enlarged blowhole ligaments are a series of diverticula. In *Hyperoodon ampullatus* and *Berardius bairdii,* the inferior vestibule is transversely divided by a dorsal fleshy fold. Rostral to the fleshy fold is the posterior portion of the nasofrontal sac and caudal to the fold is the posterior nasal sac. In species of *Mesoplodon* and *Ziphius cavirostris* that I examined, the posterior section of the nasofrontal sac was extremely reduced or absent. Thus, in *Mesoplodon* and *Ziphius,* these sacs appear to be the relatively undifferentiated homologs of the inferior vestibules and posterior nasal sacs found in delphinoids and are termed simply the posterior nasal sacs. The posterior nasal sacs are situated adjacent to the bony spiracular surface of the vertex. In *Mesoplodon carlhubbsi* and *M. bidens,* there are distinct anterior sections of both the right and left nasofrontal sacs (Fig. 5). The right sac is considerably longer than the left one and extends medially into the right nasal plug. In *M. stejnegeri,* there is a well-developed right anterior section of the nasofrontal sac, but this sac is entirely lacking on the left side (Fig. 10). In *M. densirostris, Hyperoodon*



**♀ ZIPHIUS**

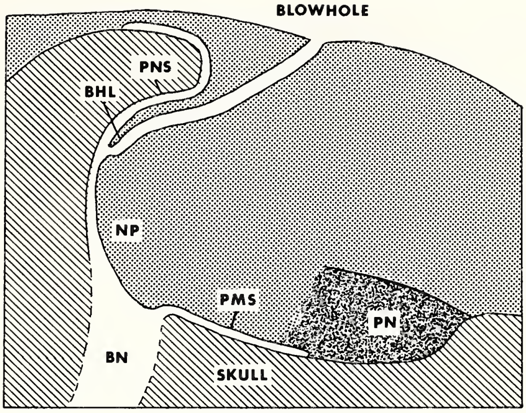
**Figure 32.** Diagrammatic parasagittal section through the right naris of an adult female *Ziphius cavirostris* to illustrate the airways. BHL = blowhole ligament, BN = bony naris, NP = nasal plug, PMS = premaxillary sac, PNS = posterior nasal sac.

*ampullatus, Tasmacetus shepherdi, Berardius bairdii,* and *Ziphius cavirostris,* these anterior segments of the nasofrontal sacs are either significantly reduced or entirely absent on both sides (Figs. 15, 21, 28).

All ziphiids examined have paired premaxillary sacs that are similar in shape to the sacs found in various delphinoids, iniids, and platanistids. The accessory sacs of ziphiids are absent or tend to be shallow blunt-ended outpockets situated just posterior to the lateral insertion of the blowhole ligament.

### Soft Anatomy

The two most superficial muscles of delphinids associated with the vestibular sac, the pars posteroexternus and pars intermedius, are lacking in all ziphiids examined. The pars anteroexternus is well developed; it originates along the facial border and inserts broadly into the connective tissue of the blowhole region. The deeper and much larger pars anterointernus has basically two insertions. The most posterior fibers wrap anteriorly around the spiracular surface of the vertex, covering all the sacs posterior to the blowhole ligament. This condition is not found in any other odontocete family. Somewhat more anterior fibers insert broadly onto the deeper connective tissue surrounding the nasal passage. The most anterior fibers insert onto the ventral and lateral aspects of the melon and grade into the rostral muscle on the rostrum. The rostral muscle itself can be subdivided into medial and lateral components similar to the condition described for delphinoids. Some of the most posterior and lateral fibers of the rostral muscle insert into the superficial tissue at the angle of the mouth. Both the amount of superficial tissue and the size of the rostral musculature controlling it are far greater than found in any delphinoid.



**♂ ZIPHIUS**

**Figure 33.** Diagrammatic parasagittal section through the right naris of an adult male *Ziphius cavirostris* to illustrate the airways. Note how enlarged the right nasal plug is compared to the female (Fig. 32). BHL = blowhole ligament, BN = bony naris, NP = nasal plug, PB = prenarial basin, PMS = premaxillary sac, PNS = posterior nasal sacs.

The melon is found in all species of ziphiids examined and is similar in position and gross appearance to the melon of delphinids. The melon in *Hyperoodon ampullatus* is situated between the enlarged maxillary crests. As in delphinids, there is a fatty core within the melon of all species of ziphiids examined that extends posteriorly into the right nasal plug but not into the left. The prenarial basin found in the crania of adult male *Ziphius cavirostris* is filled with the enlarged oily right nasal plug (Fig. 33). This condition is unique among extant ziphiids, but the prenarial basin is found in many extinct species of ziphiids. The blowhole ligaments of ziphiids are well developed. In those genera with greatly elevated vertices, these ligaments are tightly appressed against the spiracular surfaces of the vertex. This feature is unique to those ziphiids. In the adults of all ziphiid genera examined, there was a large section of hyaline cartilage in the leading edge of both the right and left ligaments.

## FAMILY PHYSETERIDAE

The family Physeteridae has three extant species within two genera (see Systematics section). The sperm whale (*Physeter catodon*) is the largest odontocete. The two diminutive species, *Kogia breviceps* and *K. simus*, are very similar to each other but distinct morphologically from *Physeter.* The facial anatomy of all sperm whales is quite complex and differs significantly from the pattern found in all other odontocetes, making interpretation of homology difficult (Mead, 1975a). I treat the subject of homology in a later section. There is a large body of literature dealing with the facial anatomy

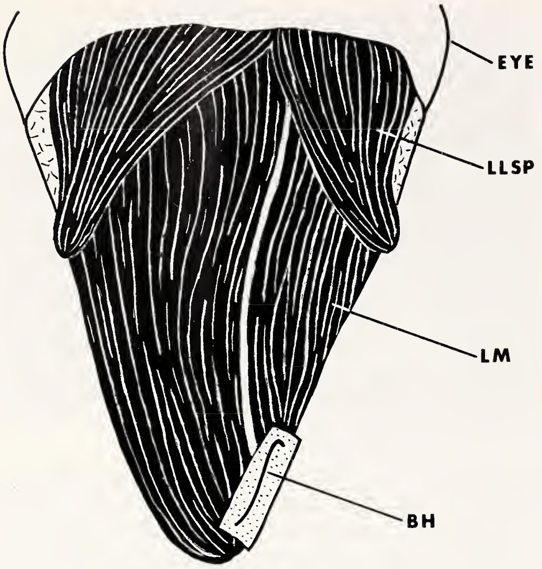


**Figure 34.** Dorsal view of the head of a fetal *Physeter catodon* (LACM 27066) with the facial muscles exposed. Note the asymmetry in the placement of the blowhole and the size of the facial muscles. BH = blowhole, LLSP = levator labi superioris proprius, LM = longitudinal muscle.

of *Physeter* (Pouchet and Beauregard, 1892; Beddard, 1923; Raven and Gregory, 1933; Clarke, 1970, 1978a, 1979; Norris and Harvey, 1972; Schenkkan and Purves, 1973; Behrmann and Klima, 1985), and of *Kogia* spp. (Benham, 1901; Kernan and Schulte, 1918; Schenkkan and Purves, 1973). In spite of this literature, many details of the facial anatomy of *Physeter* have yet to be described in detail, and due to the extreme complexity of the anatomy of *Kogia* spp., no clear synopsis of the facial anatomy is available. I therefore summarize the facial anatomy of this family in somewhat greater detail, to help clarify matters. I first describe the anatomy of *P. catodon,* then that of *Kogia* spp.

The blowhole of *Physeter* is situated at the anterior end of the rostrum, which is different from the position of the blowhole of all other odontocetes (Figs. 34, 35). It is a sigmoidally shaped longitudinal slit set distinctly off to the left side of the head. Although the blowhole is described as singular, the anterior curve of the sigmoid represents the aperture of the right nares, and the posterior curve the opening of the left nares. There is an open longitudinal furrow connecting these two openings. This nearly total separation of the two nasal passages was described long ago (Beale, 1839; Beddard, 1915, 1919), but has not been adequately noted in recent literature. Some diagrams and descriptions (Norris and Harvey, 1972) of the nasal passage system have the two nasal passages joined together and exiting at the blowhole as a single passage. This oversight has possibly led to some erroneous hypotheses regarding the mechanism of sound production; for example, Norris and Harvey (1972) stated that air could be exchanged distally from the right nasal passage to the left nasal passage via connection between the two passages. Because only a cleft open to the outside connects these two passages distally, recycling of air in this manner seems unlikely.

In the early development of *Physeter,* the external nares are paired and medially located. The blowholes become displaced to the left when the embryo attains a length of about 36 cm, and the paired blowholes coalesce before the embryo attains a length of 85 cm (Paliza G., 1964). Rarely in adults there are two distinct blowholes (Berzin, 1972).

The left nasal passage extends posteroventrally in nearly a straight line to the enlarged left bony naris. This passage is an upside down U in cross section and lacks diverticula.

The right nasal passage extends ventrally from

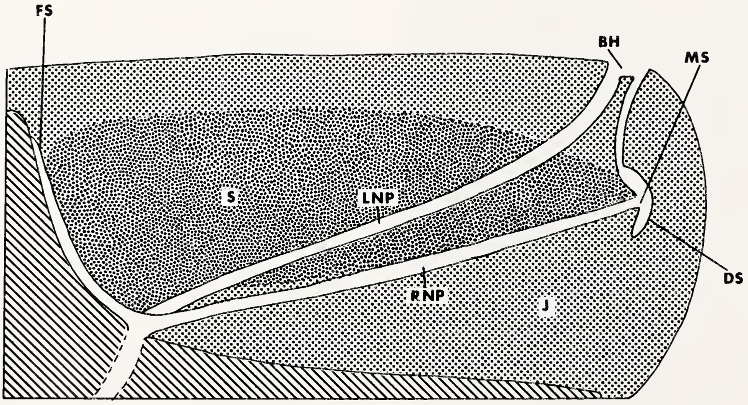


**Figure 35.** Diagrammatic parasagittal section through the head of *Physeter catodon.* Note that the nasal passages remain discrete distal till the blowhole. BH = blowhole, DS = distal sac, FS = frontal sac, J = junk, LNP = left narial passage, MS = *museau de singe,* RNP = right narial passage, S = spermaceti organ.

the blowhole and expands into an anteroposteriorly flattened ovoid sac at the anterior aspect of the rostrum. This sac has been variously called the distal sac (Raven and Gregory, 1933; Norris and Harvey, 1972), the anterior sinus (Clarke, 1970), or the right vestibular sac (Schenkkan and Purves, 1973; Clarke, 1978a). Because the term distal sac has priority and does not imply homology to sacs found in other odontocetes, I will use this term. On the posterior wall of this sac is a muscular ridge with a narrow slitlike orifice that opens to the right nasal passage. The gross appearance of this valvelike structure gives it the name *museau de singe* (Pouchet and Beauregard, 1892), or monkey's muzzle. Proximal to the *museau de singe,* the right nasal passage extends posteroventrally to the bony nares as a wide, dorsoventrally flattened tube along the ventral section of the large spermaceti case. Just superficial to the bony nares, there is another diverticulum off the right nasal passage. This flattened ovoid sac is situated against the posterior wall of the amphitheater-like skull. This sac has been called the frontal sac (Raven and Gregory, 1933; Norris and Harvey, 1972), posterior sinus (Clarke, 1970), or the nasofrontal sac (Schenkkan and Purves, 1973; Clarke, 1978a). For the same reasons as discussed for the distal sac, I prefer the term frontal sac. Along the posterior wall of this sac adjacent to the skull are numerous small fluid-filled capsules. The right nasal passage enters the right bony naris posteriorly on the skull. The left bony naris is seven times larger than the right in cross-sectional area (Norris and Harvey, 1972).

Extending from the mesethmoid to the blowholes between the nasal passages is a flattened rod of cartilage that has been interpreted as the tectum nasi (= cartilaginous septum), and surrounding the blowhole are the remnants of the cupulae nasi anteriores (Beddard, 1923; Behrmann and Klima, 1985). I was always able to find the well-developed cartilaginous septum (Fig. 37), but did not find the cupulae nasi anteriores in my dissections of young and fetal specimens.

The muscles of the facial region of *Physeter* have not been described in detail by most researchers (Pouchet and Beauregard, 1892; Schenkkan and Purves, 1973; Clarke, 1978a). Berzin (1972) provides the best detail and attempts to determine homologies between the facial muscles of *Physeter* and terrestrial mammals. I base the following on my own dissections and on the work of Schenkkan and Purves (1973), but use the terminology of Berzin (1972). There are two major pairs of facial muscles (Fig. 34). The most superficial muscle, the levator labi superioris proprius, has a broad thin origin from the occipital region of the skull and sweeps anteroventrally, becoming narrower and inserting onto the region of the lips just anterior to the angle of the mouth. The other pair of muscles, the longitudinal muscles, are much larger; each originates from the occipital crest region just ventral to the superficial muscle and extends anteriorly on the dorsolateral aspect of the rostrum. The enlarged right muscle inserts onto the *museau de singe* and the right blowhole, whereas the smaller left muscle inserts onto the left blowhole.

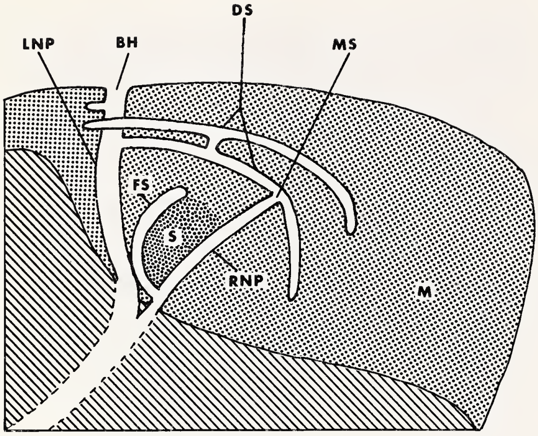
The fatty tissue in the facial region is highly modified and very distinct in structure from the melon of all other odontocetes. In adults, there is an elongate connective tissue sac, or case, that is filled with a viscous fluid called spermaceti. This is the sperm whale oil that was most sought after by the whalers. The right nasal passage passes ventral to the spermaceti case anteriorly, and through the ventral part of the case posteriorly. The spermaceti case is bordered anteriorly by the distal sac and posteriorly by the frontal sac. Below the spermaceti case is a region of connective tissue interspersed with oil called the junk by whalers because it has a lesser quantity of oil in it. Greater details of both these structures are given by Clarke (1978a). I have found that the spermaceti case of fetal and neonate specimens does not have a definitive connective tissue sheath and that the interior has substantial amounts of connective tissue in it. The descriptions of cutting into the case and of spooning out the spermaceti oil of adults are so common in the whaling literature that we may assume that the standardly described condition is true of all adults. However, my dissections show that the structure of the spermaceti organ in fetuses and young is quite different from that of adults.

The nasal diverticula of *Kogia* spp. are probably the most complex of all odontocetes, making a coherent description difficult (Fig. 36). Benham (1901), Kernan and Schulte (1918), and Schenkkan and Purves (1973) provide good descriptions, but without a specimen in hand these are difficult to follow. Detailed descriptions of some of the soft anatomy are not available. The following summary is based primarily on the above-mentioned literature and my dissections.

The single crescent-shaped blowhole is situated in the typical odontocete position dorsal to the eye region. However, the apices of the blowhole are directed posteriorly and slightly to the right, differing from the standard odontocete condition. The blowhole is distinctly set off to the left side in both species. Schenkkan and Purves (1973) stated that the blowhole is set further to the right in *K. simus;* however, raw data from Ross (1979) and my own observations do not indicate this to be true.

The left nasal passage is considerably larger than the right in diameter and is a relatively simple tube extending ventrally to the enlarged left bony nares. The only diverticulum off the left nasal passage is a small superficial posterior sac with numerous small outpockets or crypts (Schenkkan and Purves, 1973). The left nasal passage is U-shaped in cross section with posteriorly directed apices.

The right nasal passage connects to the left one through a narrow slit just deep to the blowhole. The right passage then expands into an extremely complex sac that is interpreted as homologous with



KOGIA

**Figure 36.** Diagrammatic parasagittal section through the head of *Kogia* spp. BH = blowhole, DS = distal sac, FS = frontal sac, LNP = left nasal passage, M = melon, MS = *museau de singe,* RNP = right nasal passage, S = spermaceti organ.

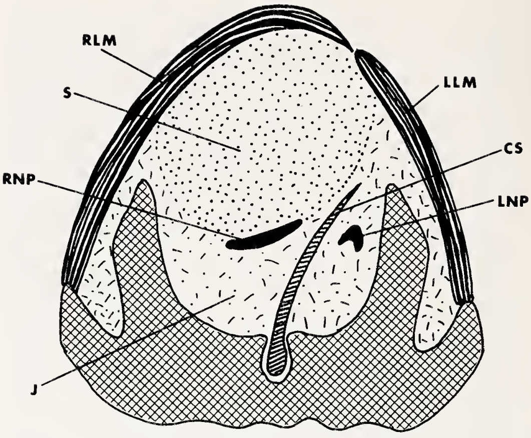


**Figure 37.** Transverse section just anterior to the bony naris of a fetal *Physeter catodon* (LACM 27066). Note that the cartilaginous septum is displaced to the left and the spermaceti organ is formed by structures from the anatomical right side. CS = cartilaginous septum, J = junk, LLM = left longitudinal muscle, LNP = left nasal passage, RLM = right longitudinal muscle, RNP = right nasal passage, S = spermaceti organ.

the distal sac of *P. catodon.* A highly simplified description of this distal sac would be that it is a diverticulum with a superior convex aspect that is partially divided into an enlarged right and a small left side, and that has a narrow connection to a deeper, parallel sac. It is this deeper part of the distal sac that connects laterally to the left nasal passage. On the floor of this sac is a raised narrow slitlike median aperture to the continuation of the right nasal passage. This slit is homologous to the *museau de singe* of *Physeter.* Sound production has been suggested as the function of the *museau de singe* in *Kogia* spp. (Wood, 1964; Norris, 1964; Caldwell et al., 1966; Backhouse, 1972; Karol et al., 1978). Deep to the *museau de singe,* the right nasal passage is a flattened tube leading to the small right bony naris. Extending from the right nasal passage just superficial to the bony nares is the large frontal sac. This sac sits adjacent to the enlarged plate on the right premaxilla and extends beyond the premaxilla laterally and dorsally. The posterior surface of the sac is densely covered with small elongate papillae averaging about 1 mm in length. The anterior surface of the sac has a smooth epithelial lining and is adjacent to the posterior aspect of the spermaceti organ.

A small spermaceti organ is present in the right posterior part of the facial region. The spermaceti organ has a distinct connective tissue sheath and is filled with a white fatty tissue. It is situated between the frontal sac and the *museau de singe* and is about 5 cm in diameter in *K. simus* and proportionately bigger in *K. breviceps.* Anterior to the nasal passages, there is a fatty region medially on the rostrum, which in gross appearance looks the same as the melon of other odontocetes. Karol et al. (1978) examined the lipid topography of the melon and spermaceti organ in *K. breviceps.* They found that the lipid content of the melon increased toward the medial core, and the spermaceti organ was filled with tissue consisting of 92–96% lipid, primarily wax esters.

The nasal plugs are asymmetrical in size, corresponding to the sizes of the respective bony nares. The enlarged left nasal plug occludes the left nasal passage from the anterior aspect, giving this passage its U-shape. The left nasal plug muscle is also considerably larger than the right nasal plug muscle.

The homologies between *Physeter catodon* and *Kogia* spp. are clear. Both have an enlarged left narial passage with only a small (*Kogia* spp.) or no (*Physeter*) diverticulum off it. The right nasal passage has a deep diverticulum, the frontal sac, and a superficial one, the distal sac. The passages converge just deep to the blowhole. The spermaceti organ is situated between the two diverticula on the right side. Anterior to the nasal passages is the fatty tissue of the typical odontocete melon, which in *P. catodon* is differentiated into the structure termed the junk by whalers.

## DISCUSSION

### HOMOLOGIES OF FACIAL STRUCTURES

The nasal diverticula and the adjacent musculature of ziphiids are so similar to those in delphinoids, iniids, and platanistids that there is little question that these structures are homologous. The nasal plugs, except for lacking lateral lips in most species of ziphiids, are almost identical in position and structure to those found in dolphins.

The premaxillary sacs are strikingly similar to those in delphinids, and in this the ziphiids resemble that group more than they do the delphinoid family

Phocoenidae. In all species of odontocetes examined or discussed in the literature, except physeterids, the premaxillary sacs are present and are similar in position and morphology.

In delphinids the inferior vestibule forms a tube that passes from beneath the blowhole ligament and turns dorsally to connect with the posterior part of the horizontally oriented horseshoe-shaped nasofrontal sac (Mead, 1975a). In *Ziphius cavirostris* and the species of *Mesoplodon* examined, the sacs that pass first beneath, then posterior to, the blowhole ligaments are not differentiated and are herein termed the posterior nasal sacs. The exception is in those species of *Mesoplodon* (*M. bidens, M. carlhubbsi,* and *M. stejnegeri*) in which the distinct, tubular anterior section of the nasofrontal sac is present. However in *Berardius bairdii* and *Hyperoodon ampullatus,* the sacs posterior to the blowhole ligament are partially divided by a ventrally protruding transverse fleshy fold of tissue. This fold divides these sacs into anterior and posterior sections. These two sacs join ventrally and connect with the nasal passage beneath the blowhole ligament. This region is homologous with the inferior vestibule described in delphinids (Mead, 1975a). This same general morphological pattern is found in phocoenids, monodontids, some iniids, and *Platanista* spp. I have used the same nomenclature, the posterior nasal sac, for the more caudal of these sacs that was used for *Phocoena phocoena* by Moris (1969). In many species of *Mesoplodon* examined, there is a small diverticula extending cranially into the posterior wall of the blowhole ligament. This resembles the position of the posterior portion of the nasofrontal sac in phocoenids. Thus, I hypothesize that the enlarged flat sac that occupies most of the space behind the blowhole ligament of *Ziphius* and *Mesoplodon* spp. is homologous with the posterior nasal sac of other non-physeterid odontocetes. The nasofrontal sac of delphinids is a complex horseshoe-shaped sac. In the specimens of *Phocoena phocoena* and *Phocoenoides dalli* that I dissected, the anterior portions of the nasofrontal sacs are continuous with the sac that is anterior to the fleshy fold, immediately posterior to the blowhole ligament. Thus, I hypothesize that this sac is homologous with the posterior aspect of the nasofrontal sac of delphinids and will use this term for these sacs in all non-physeterid odontocetes. I believe that with the elevation of the vertex in ziphiids, the sacs posterior to the blowhole ligaments became compressed in a transverse plane and the posterior nasofrontal sac became reduced and the posterior nasal sac became enlarged. I believe that the later scenario is correct, because in those species of *Mesoplodon* that have an anterior section of the nasofrontal sac, it is nearly identical with the same structure found in delphinoids. This is also the only region of any of the above-discussed complex of sacs that is too far anterior to be affected much by the evolutionary elevation of the vertex. All ziphiids have posterior nasal sacs, but the anterior tubelike section of the nasofrontal sac may or may not be present, depending upon the ziphiid species examined. The delphinid *Grampus griseus* also lacks the anterior component of the nasofrontal sac on the left side (Mead, 1975a). It seems most probable that the lack of the anterior component of the nasofrontal sac in various delphinoid, iniid, and ziphiid species represents a secondary loss, in view of the fact that other members of each family possess this structure. The accessory sacs of delphinoids appear as only slight outpocketings in ziphiids, and it is not clear whether this represents a secondary reduction of these sacs in ziphiids.

Schenkkan (1973) stated that the widened portion of the nasal vestibule is homologous with the vestibular sac of delphinoids and iniids. Schenkkan proposed that the condition found in ziphiids represents a loss of the well-defined vestibular sac as found in delphinoids. I disagree with this interpretation for the following reasons. First, the vestibule of ziphiids only widens laterally to the extent of the lateral edge of the nasal plugs and is hence not expanded in any direction into a blind-end sac as is the vestibular sac. Second, there is less subdivision of the facial muscles of ziphiids into the superficial layers of the posterior externus and intermedius, muscles that are associated with the vestibular sac of dolphins. Third, the vestibular sac of other odontocetes is located between the bony nares and the blowhole, whereas the lateral expansion of the nasal vestibule of ziphiids is adjacent to the spiracular surface of the vertex and hence much deeper in position.

Even if one accepts my conclusion that there is no true vestibular sac in ziphiids, the question still remains whether this condition represents a secondary loss of the sac or if ziphiids never had a vestibular sac. In the absence of other evidence, I invoke parsimony; it is simpler to assume that such a structure never evolved than that it evolved and was secondarily lost as suggested by Schenkkan (1973). This same argument extends to *Platanista* spp. that also lack a vestibular sac (Anderson, 1878; Purves and Pilleri, 1973).

With the above exception, the real question of homology is which, if any, of the facial structures of physeterids are strictly homologous with those found in other odontocetes. This question is quite complex and not easily answered (Benham, 1901; Mead, 1975a). Several previous workers were convinced that most, if not all, of the facial structures of physeterids discussed below are homologous with the corresponding structures in delphinoids, iniids, and platanistids (Raven and Gregory, 1933; Schenkkan and Purves, 1973; Clarke, 1978a).

The frontal sac of physeterids, which originates from the proximal end of the right nasal passage and extends as a parabolic sac along the anterior surface of the occipital crest, has been suggested to be homologous with the nasofrontal sac of delphinoids. The nasofrontal sacs of delphinoids are bilaterally paired and extend from each nasal passage posteriorly near, or adjacent to, the surface of the skull. Because the suggestion of homology is based only on gross position, it is not strongly founded, and thus I prefer the term frontal sac, because it does not imply homology. It is certainly plausible, however, that the frontal sac found in *Physeter* and *Kogia* spp. is generally homologous with the right nasofrontal sac/posterior nasal sac/inferior vestibule complex of other odontocetes. If this is true, it would imply the total disappearance of the diverticula on the left side.

The distal sac, which is a diverticulum off the right nasal passage, has been suggested to be homologous to the vestibular sac of delphinoids and iniids. The vestibular sac of these small dolphins is an unpaired, or only partially bilaterally divided, diverticulum that occurs as an expansion of the single distal nasal passage. The joining of the nasal passages is obviously a derived feature. In physeterids, the nasal passages remain separate distally to just deep of the blowhole, and the distal sac is clearly a diverticulum arising from the right nasal passage exclusively. The extent to which the nasal passages remain separate in physeterids is most likely a primitive condition and this orientation of the sac makes it seem unlikely that it is a homolog of the true vestibular sac. Hence, I feel that it is a neomorph in physeterids.

My dissections and most published accounts indicate that there are no premaxillary sacs present in physeterids. Schenkkan and Purves (1973) stated that there is a small premaxillary sac present in *Kogia* spp. on the left side. I found that the epithelium is loose over the premaxilla adjacent to the left nasal plug, which allows the plug to be retracted from the bony nares freely, but there is no discretely formed sac in this region.

It has been remarked that the ziphiids possess a spermaceti organ similar to that found in physeterids (Gray, 1882; Tomilin, 1967; Wood and Evans, 1980). For the genera *Berardius, Tasmacetus, Hyperoodon,* and *Mesoplodon,* I have found no structure that even remotely resembles the spermaceti organ of either *Physeter* or *Kogia*. The melon and the spermaceti organ have been considered to be homologous (Howell, 1930), but the definitions of these structures were not specified. Mead (1975a) suggested that the term spermaceti organ should be reserved for the discrete, fat-filled organ that is surrounded by a sheath of connective tissue. Schenkkan and Purves (1973) believed that the spermaceti organ arose as a new structure, because it is located posterodorsal to the right nasal passage and the melon is located anteroventral of the nasal passages. A combination of these two criteria provides an excellent definition for the spermaceti organ. The position of the junk in *Physeter* and the appearance of the tissue in this region of *Kogia* spp. suggest to me that this tissue is truly homologous with the melon found in other cetaceans. The only structure that even vaguely resembles the spermaceti organ is the adipose structure found in the prenarial basin of adult males of *Ziphius cavirostris*. Norris and Harvey (1972) briefly commented that this structure may be homologous to the true physeterid spermaceti organ. However, because it is clearly situated anterior to the nasal passages, it cannot be homologous with the spermaceti organ and is in fact the enlarged right nasal plug.

The facial anatomies of both *Physeter catodon* and *Kogia* spp. are extremely different from the anatomical pattern found in other odontocetes. With such extreme differences, it is difficult to tell whether a structure in a given genus has evolved into a highly modified feature that has little resemblance to the primitive form of a structure inherited in common, or if a structure has evolved de novo and is hence not homologous to any feature. This question is important because the correct interpretation will elucidate much about the evolution of these structures and about their possible functions, and it may be quite useful in a phylogenetic analysis of the odontocetes. In such an analysis, when in doubt, it is better not to imply homology; if the structures are truly homologous, one only lacks information, but if homology is incorrectly implied, then erroneous data are added to the analysis.

## EVIDENCE FOR SOUND PRODUCTION

The complex facial construction of odontocetes undoubtedly serves a number of functions. Clearly, a primary function is one of respiration. Odontocetes must surface to exchange the gases in their lungs at intervals ranging from less than one minute for many delphinoids to over an hour for *Physeter catodon* (Tomilin, 1967) and *Hyperoodon ampullatus* (Benjaminsen and Christensen, 1979). Cetaceans are able to exhale and inhale nearly 85% of their lung tidal volume (Scholander, 1940) in approximately one second (Lawrence and Schevill, 1956) during their brief contact with the air. During submersion, it is important that a tight seal be maintained in order to prevent the entrance of water into the lungs. Mechanoreceptors around the blowhole and along the superficial portions of the nasal passages may provide sensory input necessary to determine when the blowholes have cleared the water/air interface (Bryden and Molyneux, 1986). However, the complex series of nasal diverticula and adjacent soft structures of odontocetes seem too complicated merely to function as an efficient terminal respiratory valve. Mysticetes lack this complex facial anatomy and are capable of diving to at least 500 m (Howell, 1930). Many pinnipeds are also capable of deep dives, some up to 600 m (Kooyman, 1966), yet they also lack any extreme anatomical modification of the nasal anatomy. It is highly likely that some new nonrespiratory function provided the evolutionary selective forces that shaped this complex region.

There are two main theories regarding the specific, nonrespiratory function of the facial region. The first is that facial structures are responsible for the production of sounds utilized for echolocation. The second is that this region, at least in sperm whales, plays some role in buoyancy control. The hypothesis of buoyancy control by regulating the amount of air within various sacs (Raven and Gregory, 1933; Schenkkan and Purves, 1973) is not widely accepted. The hypothesis that the function of the spermaceti organ itself is the control of buoyancy (Clarke, 1970, 1978b, 1979) has serious flaws as pointed out by various authors (Ridgway, 1971; Schenkkan and Purves, 1973). I shall discuss only the sound production theory, the idea favored by most researchers today and relevant to most, or all, odontocetes.

The literature on cetacean sounds is voluminous, and I do not attempt to summarize it here. Odontocete phonations, however, can be classified basically into two categories: whistles and echolocation sounds (Popper, 1980). Whistles are sounds typically under 20 kHz that are narrow-band tones of continuous frequency. Whistles have been suggested to function in communication, although there are several species in virtually every odontocete family that are believed not to whistle (Herman and Tavolga, 1980). The echolocation sounds are described as short broad-band pulses of high frequency. These sounds are often described as clicks and buzzes. It is documented that both whistles and clicks can be produced simultaneously and that each sound can begin or terminate independent of the other sound (Lilly and Miller, 1961). This is cited as strong evidence that there are at least two sites of sound production in odontocetes. It is often suggested that the echolocation clicks and buzzes are produced by some component of the facial region although a few researchers contend that these sounds are produced in the laryngeal region. Mead (1975a) and Dormer (1979) provide reviews of prior papers dealing with the anatomical source of delphinid echolocation sounds.

The source of the whistle sounds is unknown, although some suggest that they are produced in the laryngeal region, whereas Norris et al. (1971) and Dormer (1979) provided some cineradiographic evidence that the right nasal plug is the source of clicks and the left nasal plug may be the source of the whistles. Some evidence to support this hypothesis has been published recently. Click emission in *Phocoena phocoena* is accompanied with the formation of small bubbles along the edge of the right nasal plug (Amundin and Andersen, 1983). In *Delphinapterus leucas,* whistle production is often associated with an escape of air along the left posterior edge of the blowhole (Ridgway and Carder, in press).

The evidence that the facial region is responsible for the production of sound comes from many sources that fall broadly into two categories: anatomical and experimental. Up until 15 years ago, virtually all the evidence was based on anatomical studies. The basic premise was that of correlation and implied causation. It has been suggested since the mid-twentieth century that dolphins might echolocate (Kellogg et al., 1953; McBride, 1956). The ability of the delphinid species *Tursiops truncatus* to echolocate was demonstrated experimentally by Norris et al. (1961). Subsequently, all odontocete species examined have been found to produce high frequency clicks, and all species are now presumed to produce such sounds and utilize them in echolocation, although there is no behavioral evidence that sperm whales actually echolocate while diving (Watkins, 1980). Mysticete cetaceans also have a wide repertoire of sounds, but these are typically of low frequency and probably associated with communication (Thompson et al., 1979). Most researchers believe that mysticetes cannot echolocate, but Beamish and Mitchell (1973) suggested that the minke whale (*Balaenoptera acutorostrata*) can produce sounds that are potentially suitable for echolocation. The only experimental data for any mysticete suggest that humpback whales (*Megaptera novaeangliae*) probably cannot echolocate (Beamish, 1978). As stated earlier, only odontocetes have the complex series of nasal passage diverticula and complex associated soft structures, and it was therefore believed that this anatomical region is the source of the clicks and buzzes.

The experimental data are more recent and encompass several design approaches. One approach was to remove a live dolphin from the water and view with radiographs the laryngeal and facial regions during sound production. Preliminary results, obtained with high-speed cineradiographs, were presented by Norris et al. (1971), and more complete results of this technique were described by Dormer (1979). Their results were based primarily on whistle-class sounds. The sequence of such phonation involves first a filling of the airspace in the respiratory system between the larynx and the nasal plugs; this space is termed the nasopharyngeal airspace (Fig. 38). With the epiglottic spout of the larynx tightly shut, the palatopharyngeal muscle then contracts; this decreases the volume of the nasopharyngeal airspace and forces the air up through the bony nares into the distal nasal passages. The premaxillary sacs quickly fill with air, and soon after, the inferior vestibule and nasofrontal sacs also fill. There is then a noticeable pulsation in the left nasal plug; this occurs concurrently with the production of whistles. The vestibular sac fills with air during this process, and the anterior portion usually remains filled with air during an entire series of phonations. However, the enlarged posterior portion of the vestibular sac is emptied of air between phonations. This has been interpreted to indicate that the anterior aspect of this sac functions as a reflective surface by providing a distinct air/tissue interface, whereas the larger posterior portion functions as a terminal reservoir for air to be recycled.

Dormer (1979) was able to record events during the production of clicks on a few occasions. The results were limited, but it was shown that there is also a decrease in the nasopharyngeal airspace by

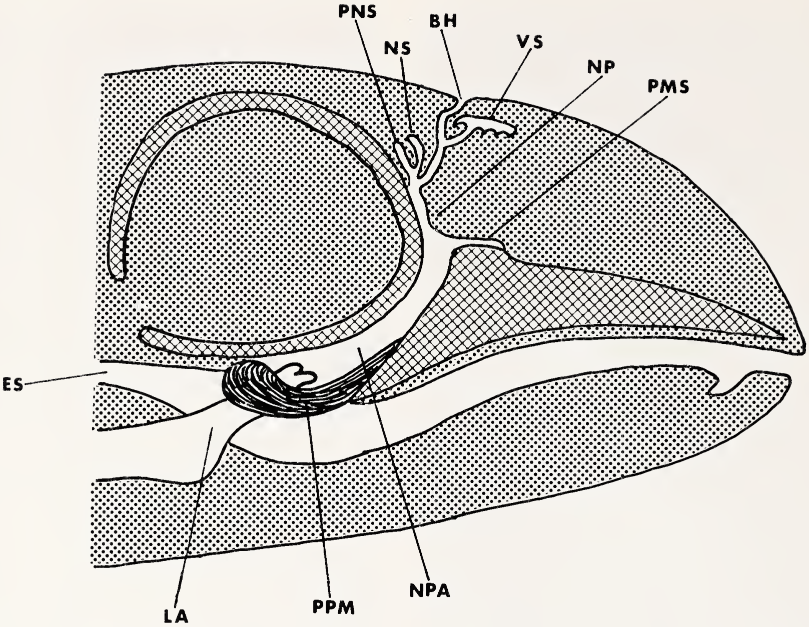


**Figure 38.** Diagrammatic sagittal section through the head of a porpoise, *Phocoena phocoena*. Stippled areas represent soft tissues and crosshatched areas represent bone. BH = blowhole, ES = esophagus, LA = larynx, NP = nasal plug, NPA = nasopharyngeal airspace, PMS = premaxillary sac, PNS = posterior nasal sac, PPM = palatopharyngeal muscle, NS = nasofrontal sac, VS = vestibular sac.

the contraction of the palatopharyngeal muscle during emission of such sounds, although at a lesser rate than during the production of whistles; this indicates that echolocation sounds require less air than do whistles and hence can be emitted for a longer duration before air must be recycled. Both nasal plugs were apparently seated against the bony nares, and no movement of the plugs could be detected. Because the vestibular sac was expanding however, there must have been air passing across some surface of the nasal plugs. Norris et al. (1971) and Dormer (1979) concluded that whistles were produced by the left nasal plug and that clicks were produced by the right nasal plug. During all observations, the laryngeal cartilages were not observed to move during any part of the phonation process. Hollien et al. (1976) also experimented with live phonating dolphins, using still radiographs. These researchers could detect different changes within the facial region during the production of clicks and whistles. However, the resolution was not adequate to provide good details. All these studies found that there was no perceivable movement or vibration in the larynx.

Using a somewhat more sophisticated technique, Mackay and Liaw (1981) used ultrasonic imaging and Doppler shifts to examine phonating dolphins is a manner similar to the previous studies. They found that during the production of clicks, the nasal plugs and air sacs vibrated, whereas no vibration in the larynx could be detected. They also noted that the nasal diverticula on the right side always vibrated, but that those on the left side vibrated only infrequently. The vestibular sac increased in volume steadily during phonation. Once again, there was no evidence that the larynx is directly involved, at least in the production of clicks.

By placing an array of sound transducers on the facial region of click-emitting dolphins, Diercks et al. (1971) used triangulation to pinpoint the sound source. Assuming that the sound was transmitted in a straight line, they found that the clicks were being produced in the region of the nasal plugs.

Although the above evidence strongly suggests that the facial architecture is responsible for the production of sound, it is still conceivable that the sound is produced elsewhere (e.g. in the larynx) and merely transmitted through the facial region causing structures there to vibrate. It is also conceivable with the above evidence that the nasal diverticula are only air reservoirs and that sound is produced in the larynx. In short, the above provides good evidence for sound production in the facial region, but it does not absolutely rule out the larynx as the source of sounds.

Conclusive evidence against the larynx as the site of sound production comes from electromyographic data and measurements of air pressure differences in the upper respiratory system (Ridgway et al., 1980). Electromyographs of the palatopharyngeal, hyoepiglottal, intercostal, and various facial muscles were made simultaneously with sound recordings from dolphins. The intercostal and hyoepiglottal muscles, important in human laryngeal sound production, were not active during the production of clicks and whistles, but were active during the expulsion of large amounts of air through the blowhole. The palatopharyngeal muscle was often active during phonation, but not as consistently as the facial muscles. Activity of the pars anterointernus, pars posterointernus, nasal plug muscles, and diagonal membrane muscles was consistently associated with phonations. Facial muscles on both sides of the head fired simultaneously, and different parts of the pars anterointernus had similar EMG patterns. The only exception was the diagonal membrane muscle, in which the right side fired more consistently and for longer periods than the left during the production of chirps and click trains.

These researchers (Ridgway et al., 1980) also placed catheters at various positions within the nasal passages and the trachea to record air pressure during phonations. Between breaths, there was a constant 25 mm Hg pressure within the trachea, but a distinctive intranarial air pressure increase was recorded during phonation. This provides conclusive evidence that the larnyx must be closed during phonations in order to maintain a higher pressure in the nasopharynx and nasal passages than in the trachea. Open cathethers that equalized the pressures of airspaces and the outside were placed in various positions in the nasal passages and diverticula. When these were placed in the premaxillary or vestibular sacs, the dolphins were still able to phonate, indicating that high pressures within these sacs were not necessary for sound production. However when a catheter was placed in the nares (bony nares?), the animals were not able to produce either whistles or clicks. If the larynx is the site of sound production, a catheter in the respiratory system distal to the larynx should not prevent phonations. Small inflated balloons were also placed in various positions in the narial airspaces; these had no effect on phonation, indicating that sounds were not produced by the resonation of air within spaces, but are caused by vibrations of adjacent soft tissues. Subsequent researchers came to the same general conclusions based on intranarial air pressure and electromyographic data from click-emitting *Phocoena phocoena* and *Tursiops truncatus* (Amundin and Andersen, 1983).

The above review of the evidence for sound production as a function of the facial region of delphinids is necessary in light of Purves and Pilleri's (1983) recent advocacy of the larynx as the site of sound production. Their stated purpose is "an attempt to correct some of the prevalent ideas about vocalization in whales and dolphins, which have been arrived at without an intimate knowledge of cetaceans and without due regard to underwater acoustics" (Purves and Pilleri, 1983). To refute them fully is beyond the scope of the present work; however, the following major flaws are noteworthy. Purves and Pilleri refute the evidence for the facial region as the source of sound production through the use of erroneously constructed models. The first three models (Purves and Pilleri, 1983:figs. 2–4) are based on sound being produced by resonation of air within the nasal passages, an idea that has been out of favor for over a decade. Their fourth model, more in step in that the nasal plugs are postulated as the possible source of sound, is refuted on the grounds that the acoustical lens idea proposed by Norris (1964) would scatter, not focus, the sound. Purves and Pilleri then state themselves (1983) that sound cannot be focused in this manner. Additionally, their model of the melon is based on diagrams by Norris (1964, 1969), although it is well known that the melon is actually more complex in lipid topography and extends posteriorly into the right nasal plug, the site suggested as producing the clicks of echolocation (Litchfield et al., 1973; Mead, 1975a). Purves and Pilleri disregarded the fact that Ridgway et al. (1980) found no rise in intratracheal pressure during phonation by stating "Had they measured the interlaryngeal pressure the results might have been quite different" (Purves and Pilleri, 1983:74). Because the larynx and trachea form a small continuous rigid-walled tube (Fig. 38), it is inconceivable that air pressure can fluctuate significantly in one region and remain constant nearby. Behrmann (1987) could not achieve experimentally the expansion of the laryngeal sacs proposed as a sound-producing mechanism by Purves and Pilleri. Lastly, Purves and Pilleri (1983) did not cite and evaluate most of the previously mentioned experimental evidence for the source of phonation sounds, or they merely stated that the evidence is irrelevant. Recently, Norris (1986) provided a brief but accurate rebuttal to this book. Yet neither Norris's review nor my comments above cover in detail the copious technical and logical errors in Purves and Pilleri's (1983) book.

Due to differences in the construction of the nasal passages and adjacent soft structures, the exact mechanism of sound production in delphinids is not applicable to ziphiids. The vestibular sac of delphinids is hypothesized to function as a terminal reservoir for air that could be recycled back to the nasopharyngeal airspace after phonations. Because ziphiids lack a vestibular sac, they cannot store and recycle air in this manner. Either air must be lost out the blowhole after it is used for phonations or it must be stored elsewhere in the nasal passages. It would seem unlikely that air would be lost through the blowhole because this would severely limit the number of times an animal could either comunicate or echolocate during a dive before too much air was lost to produce sounds. It seems more likely that there is an air reservoir elsewhere. I suggest that the posterior nasal sacs could function in this capacity, because they are relatively enlarged and are the most distal of the nasal diverticula of ziphiids.

Another difference between delphinids and ziphiids in regard to sound production is the structure of the blowhole ligaments. The condition found in ziphiids in which the rigid blowhole ligaments are tightly appressed to the spiracular surface of the vertex appears well suited for sound production.

The forcing of air past the blowhole ligament into the posterior nasal sacs could cause them to vibrate. These vibrations may be transmitted to the nasal plugs that are tightly abutted against the blowhole ligament when the nasal plug muscles are relaxed. Several dissections revealed fatty tissue, the elliptical bodies, similar to that found in the right nasal plug also adjacent to the right nasal plug on the anterior surface of the right blowhole ligament. This suggests that sound could travel from the blowhole ligament through this fat. The posterior fibers of the pars anterointernus muscle are situated such that, when they contract, they would compress the posterior nasal sacs against the spiracular surface of the vertex and force any air within the sacs out past the blowhole ligaments into the main nasal passages. The position and size of the pars anterointernus suggest to me that the air that passes beneath the blowhole ligaments causing them to vibrate may pass in the opposite direction. During a relaxed phase, air is passed into the posterior nasal sacs; then the contraction of the pars anterointernus muscles would force air past the blowhole ligaments resulting in phonation. Because the above hypothesis is based only on anatomical evidence, it must be viewed with some caution.

The above model of sound production in ziphiids provides some insight into the functional significance of an elevated vertex. Slightly elevated vertices are found in the skulls of advanced kentriodonts (Barnes, 1978) and the modern ziphiids *Berardius* and *Tasmacetus.* The remaining ziphiids have moderately to extremely elevated vertices. An elevated vertex is accompanied by the elevation of the posterior section of the facial fossa. This provides the facial muscles in this region to be oriented in a nearly horizontal plane with the fibers situated anteroposteriorly. This is clearly seen for the pars anteroexternus in Figures 6 and 22, and for the pars antrointernus in Figures 7 and 23. The posterior facial muscles of most delphinoids are oriented in a much more vertical plane. The muscle fibers that originate in the anterior facial fossa of both delphinoids and ziphiids are situated in a nearly vertical plane. Therefore, ziphiids with elevated vertices have both muscle fibers that insert onto the nasal passage and diverticula that are both horizontally and vertically oriented. This probably provides for different muscular control over this region than is possible with muscles that are oriented only in a primarily vertical plane.

It would be useful to attempt to correlate differences in facial anatomy with differences in sounds produced among species of odontocetes. However, this would require a better understanding of the exact mechanism of sound production. It would also require a rather complete knowledge of the sound repertoire of a species in the wild, which is only known for a very few species. For ziphiids, the only published recordings of sounds are a few of *Hyperoodon ampullatus* (Winn et al., 1971) and of a moribund *Mesoplodon densirostris* (Caldwell and Caldwell, 1971).

## CRANIAL AND FACIAL ASYMMETRY

Typically, mammals are bilaterally symmetrical in most aspects of their anatomy. An exception to this is found in the viscera that have secondarily become elongate and rotated in higher vertebrates. The viscera of cetacea are asymmetrical as well (Slijper, 1958; Arvy, 1977). Most other observed asymmetry in mammals is usually either negligible or pathological, and the skew is not consistently to one side (Howell, 1925). An important exception to this generality is in the facial region of most odontocete whales.

The order Cetacea comprises three suborders, the extinct Archeoceti, the Mysticeti or baleen whales, and the Odontoceti or toothed whales. Most cetacean systematists believe that the order is monophyletic and that the two modern suborders are derived from the archeocetes (Van Valen, 1968; Árnason, 1969, 1974; Árnason et al., 1984; Duffield-Kulu, 1972; Barnes and Mitchell, 1978; Fordyce, 1980; Barnes et al., 1985). The archeocetes that lived during the Eocene and early Oligocene possessed skulls that were essentially symmetrical (see Kellogg, 1936). Modern and fossil baleen whales also all appear to have symmetrical skulls. Fossils of the suborder Odontoceti can be found in rocks of the Oligocene to the Recent, and the suborder is variously subdivided into numerous families (Slijper, 1936; Simpson, 1945; Barnes et al., 1985). The marked and sometimes very pronounced asymmetry found in most odontocetes has been discussed by many authors (Kükenthal, 1908; Miller, 1923; Winge, 1942; Ness, 1967; Norris, 1964; Mead, 1975a).

The purpose of this section is threefold: (1) to review the nature and extent of cranial and facial asymmetry in odontocetes, (2) to present a new hypothesis as to the function of this asymmetry, and (3) to discuss cranial and facial asymmetry from a systematics viewpoint. For the purposes of this discussion, I use the term cranial asymmetry for any deviation from a symmetrical pattern visible in the bones of the skull, and the term facial asymmetry for the same deviation observed in the facial soft anatomy. The separation of these two terms is important because it is possible to have facial but not cranial asymmetry, and only cranial asymmetry is detectable in the fossil record.

Ness (1967) attempted to describe and quantify the asymmetry of the skull more thoroughly. He defined cranial asymmetry in odontocetes as the medial anatomical deviation from the geometric midline of the skull and defined the skew of the skull as the proportion of midline deviation to the condylobasal length of the skull. Hence, his description of asymmetry involved an absolute measurement, and the measure of skew was scaled for size. His comparisons within and between families were based on the skew, and his analysis yielded an asymmetry sequence of *Kogia* > monodontids > delphinids (excluding *Orcinus*) > ziphiids > *Orcinus.* Ness also stated that he had noted a positive correlation between the absolute size of skulls and degree of skewing.

Several flaws in Ness's analysis led him to these erroneous conclusions. First, although his measurement of asymmetry is quite simple and readily repeatable, it does not reflect all the major aspects of asymmetry. The asymmetry of the skull has basically two easily quantifiable components, the deviation of medial sutures from the midline of the skull and the size and/or shape difference between corresponding bilateral structures. I shall use the term asymmetry here in the more general sense of any measurable differences between bilateral structures; this includes size or shape differences as well as medial deviation. I shall use the term skew also in the more conventional context as meaning a directional deviation from the geometric midline of the skull. As will be demonstrated below, both terms are useful and both can be quantified and scaled to make meaningful comparisons between animals of different size.

In most delphinids, the medial sutures do not deviate much from the midline (small skew), yet the right premaxilla at the narial region is always significantly larger and extends farther posteriorly than the left premaxilla in the same region. This point is even more dramaticaly exemplified by the beaked whale *Ziphius,* which Ness describes as having little skew but which in fact exhibits one of the greatest degrees of asymmetry among odontocetes in the shape and size of the premaxillae. The best way to quantify size and/or shape differences in bilateral structures is to measure each structure at comparable locations. This can then be scaled by using a ratio of the right side to the left side for easy comparisons between taxa. For example, a measurement of width of both the premaxillae at the anterior edge of the bony nares would be quite informative for most odontocetes. In many phocoenids however, the bilateral structures may be nearly identical in shape and size but deviate from the midline slightly to the left. This variation in the nature of cranial asymmetry makes quantifiable comparisons somewhat difficult. Another point to recognize regarding asymmetry is which region of the skull one is using for comparison. The greatest deviation from the midline tends to be in the region of the postnarial nasals, except in *Kogia* (Ness, 1967), yet the nasals themselves are usually about equal in size. As stated previously, the premaxillae tend to vary more in size and shape lateral and anterior to the nares, but are less skewed. In discussions and comparisons of the asymmetrical features of the skull, it is important to compare the entire suite of characters.

Ness's measurement of skew has the additional inherent problem of using the proportion of medial deviation to condylobasal length. Cranial asymmetry is essentially limited to the facial region around the bony nares and is not noticeably present on the rostrum. Because this measurement is essentially a ratio, care must be exercised not to compound the desired measurement with another varying character. The ratio of rostrum length to condylobasal length is quite variable among cetacean species in correlation with the differing dental batteries and correspondingly different feeding strategies. Theoretically, two odontocete species with equal absolute medial deviation and equal braincase size (e.g. similarly sized animals), but with extremely different rostral lengths, could have quite different skews using Ness's methods. If such a proportion is to be used to establish a relationship between skew and absolute size of skulls, the rostrum should not be included, and the ratio of deviation to braincase width or length, or some measurement of angle (e.g. Perrin, 1975, measurement #41), would be appropriate. As a rule in delphinids, most smaller species (e.g. *Delphinus, Stenella, Sotalia*) have proportionately longer rostra, and therefore smaller skews, than do the larger species (e.g. *Globicephala, Grampus, Pseudorca*), and hence Ness's statement regarding the relationship of size to degree of skewing may reflect, at least in part, the relationship of proportional rostral length to absolute skull size.

The various theories regarding the function of cranial and facial asymmetry have a long history and were well covered and discussed by Mead (1975a). After reviewing the literature and completing careful dissections of the facial region of numerous odontocetes, Mead concurred with Norris (1964) and Wood (1964) that the asymmetry is related to some aspect of sound production from this region of the head, and he suggested that there might be some division of function between the distal nasal passages, with one part specialized for the production of sound and the other maintaining the primary role of respiration. High-speed cinematography of the breathing of a *Tursiops* showed that the left narial passages remained open slightly longer than the right during inhalation (Lawrence and Schevill, 1956).

In the following hypothesis, I suggest a functional advantage of the asymmetry of the nasal sacs and surrounding structures, and of the corresponding underlying parts of the skull. It is based on the assumption that the facial region is the source of at least the clicks and buzzes produced by odontocetes for echolocation and perhaps communication.

The nasal sacs, except the vestibular sac, and the nasal plugs of most odontocetes are paired structures that occupy the region from the bony nares distal to the single blowhole. It would be logical to assume that originally both of the bilaterally paired structures contributed equally to the production of sound. Because the paired structures would undoubtedly have been slightly different from one another, it is probable that they would have produced, simultaneously, sounds of slightly differing frequency and/or period. This production of two sound waves that differed slightly might have had the effect of attenuating or cancelling out some of each other's energy, or producing an echo location signal that is unclear. In order to produce a clear sound with no attentuation due to slight physical differences in sound waves, it is important to have a single sound source. The advantages of having only one source producing all the sound would bring about selection for the enlargement of that side (e.g. the right) and hence produce asymmetry. This enlargement would tend to displace the structures on the other side farther from the midline so that the sound-producing structures would not be significantly off to one side and hence produce a very asymmetrical sound field. Interestingly, the sound fields produced by the odontocetes studied are slightly asymmetrical (Purves and Pilleri, 1983).

The hypothesis presented here is supported by the following evidence. First, only in cetaceans that are known or suspected to produce echolocation sounds are the skulls and facial anatomy asymmetrical. Mysticete whales lack both the asymmetrical skulls and apparently the ability to produce the high-frequency sounds necessary for echolocation of good resolution. Mysticete whales also lack the complex nasal sac system and corresponding structures in the facial region. Second, only those structures associated with the nasal passages and diverticula are asymmetrical; all other aspects of the braincase and rostrum are symmetrical, except in *Monodon monoceros* in which the left maxillary tooth enlarges in adult males. During ultrasound observations of echolocating dolphins in captivity, Mackay and Liaw (1981) found that the diverticula vibrated always on the right side and infrequently on the left side. Additionally, the deep-diving species such as the physeterids and ziphiids as well as the blind river dolphin *Platanista* show the greatest degree of asymmetry. This would be in accordance with the above reasoning, because these species are navigating in virtually aphotic or turbid waters and theoretically must rely heavily upon echolocation. This hypothesis certainly does not exclude the idea summarized by Mead (1975a), that one side functions primarily for respiration and the other for phonation.

Cranial asymmetry is not universal within the Odontoceti in either presence or extent. When present however, the skew is always to the left side. The most primitive family of odontocetes, the Agorophiidae, had symmetrical skulls (Whitmore and Sanders, 1976; Fordyce, 1981; pers. obs.). Other primitive odontocete families, Squalodontidae and Rhabdosteidae (= Eurhinodelphidae), also appear to have had symmetrical skulls, but Winge (1942) suggested, without providing evidence, that the beginning of asymmetry can be found in the Squalodontidae. Due to compressional distortion of fossils, it is difficult to detect very slight degrees of asymmetry. If cranial asymmetry did have its beginning with the squalodontids as Winge suggested, then it is even more interesting to note that Fleischer (1976) found the first evidence of the ability to receive high-frequency sound, based on his studies of cochlear structure, also in squalodontids. The Agorophiidae were extinct by the end of the Oligocene, and the latter two families were extinct by the middle Miocene (Barnes et al., 1985).

Extant odontocete familes have fossil representatives at least as old as late Miocene. All modern odontocetes have asymmetrical skulls. Several authors (Ness, 1967; Barnes, 1985a) have stated that the modern iniid *Pontoporia blainvillei* has a truly symmetrical skull. I measured the transverse width of the premaxillae in the narial region in a small series of *P. blainvillei* (N = 14) and in all cases the right premaxilla was wider than the left. At the anterior margin of the naris, the left premaxilla averaged 90% the width of the right, and at the posterior contact of the premaxilla with the naris, the left premaxilla averaged 91% the width of the right. *Pontoporia blainvillei* has extremely asymmetrical nasal sacs and musculature (Schenkkan, 1973; Mead, 1975a). Both the physeterids and ziphiids have fossil members with asymmetrical skulls as old as the early and middle Miocene, respectively, with most modern species having extremely asymmetrical crania. The Delphinoidea consists of the modern families Delphinidae, Phocoenidae, and Monodontidae, and the extinct families Kentriodontidae and the monotypic Albireonidae. The skulls of specimens from both these extinct families are reported to have symmetrical, or nearly so, facial regions (Barnes, 1978, 1984). However, in examining fossils from both groups, I found that at least *Albireo whistleri* and the advanced kentriodontid genera, *Lophocetus* and *Delphinodon,* have slightly to moderately asymmetrical skulls in that the premaxilla is larger on the right side than on the left side. This is quite clear in the photograph of the kentriodontids *Lophocetus repenningi* (Barnes, 1978:20) and *Lophocetus pappus* (Kellogg, 1955:pl. 1).

Both cranial and facial asymmetry are found in all the modern representatives of the odontocete families Physeteridae, Ziphiidae, Delphinidae, Monodontidae, Phocoenidae, Iniidae, and Platanistidae, but fossil evidence indicates that cranial asymmetry is less pronounced in the more primitive members of these groups and totally absent in some extinct groups. If these families are monophyletic, as suggested later in this paper, then in view of the fact that the more primitive members seem to have nearly symmetric skulls, one needs to ask whether asymmetry is a parallelism or a synapomorphic character. Because intermediate fossils are lacking, facial asymmetry is impossible to detect, and slight cranial asymmetry is difficult to determine, the paleontological record cannot answer this question at this time. However, hypothetically, beginning with a symmetrical head and a selective advantage in asymmetry, there should be a 0.5 chance of skewing to the left. Because the members of all seven families skew to the left the random chance that these seven events were independent (parallel evolution) would be less than 0.01%, below the standard statistical significance level of 0.05%. It is safe to say that it seems highly improbable that asymmetry evolved independently in all the families. The probability increases if it is assumed that asymmetry arose only two or three times in the evolution of the odontocetes, but it is more easily conceivable that the common ancestor of all modern odontocetes had asymmetrical facial soft structures that had not yet affected the underlying skull and hence cannot be detected in the fossil record (Mead, 1975a; Fordyce, 1981). A modern analog to this situation would be the case of *Pontoporia* that has a slightly asymmetrical skull but possesses a very asymmetrical facial soft anatomy. This might also explain the different patterns of cranial asymmetry observed in odontocetes. If the facial anatomy was first in developing asymmetry for whatever function early in odontocete evolution, and bone is usually modified in response to changes in the soft anatomy, then it would follow that facial asymmetry would eventually produce cranial asymmetry. This secondary evolution of cranial asymmetry could be produced in slightly different ways. Additionally, all modern odontocetes except the physeterids have basically the same pattern of asymmetric nasal diverticula and corresponding asymmetry in these structures (Mead, 1975a; Schenkkan, 1973), indicating that these structures were present in the common ancestor to these groups. Physeterids also have a complex nasal sac system, but it is so derived that it is hard to determine what structures are homologous to the structures evident in other odontocetes (see Homology section for full discussion).

If the feature of asymmetry is primitive for all modern cetaceans as argued above, then there ought to be a reevaluation of previous systematic works in which the character of facial and/or skull asymmetry was used as a derived character at a lower taxonomic level. For instance, Barnes (1985a) used asymmetry as his only synapomorphy to differentiate the family Pontoporiidae from all other odontocetes cladistically. Although he did list other characters in the family diagnoses, he did not state the polarity of these characters, and it is unclear which features are considered derived and which are considered primitive.

## SYSTEMATICS

### INTRODUCTION

Most previous higher-level systematic works on the Odontoceti have placed the extant families within three or four superfamilies and have not resolved the relationship among these superfamilies. For the most part, membership in these superfamilies has been based on general morphological similarity or even habitat. Thus, most current classifications are based on diagnoses that are a combination of primitive and derived characters (Rice, 1984), and to date only one phylogenetic analysis among the families of the Odontoceti has been attempted (de Muzion, 1984).

The various structures of the facial region are well suited as characters for use in a phylogenetic analysis at the level of families because they vary consistently between taxa and are not ecophenotypic (Wiley, 1981). In addition to facial structures, I have also evaluated and used other morphological characters in this analysis. Morphological data have certain inherent advantages, particularly for rare species from which it is difficult to obtain adequate samples for various biochemical analyses. Other advantages of morphological data include the availability of osteological specimens that are collected over a long period of time and can be compared directly with fossils to increase taxonomic diversity for outgroup analysis. In addition to the outgroup method, data from fossils also assist in helping to determine character polarity by directed chronoclines and morphoclines. Morphological data can be evalulated cladistically and reflect a large (but unknown) portion of the genome.

The scope of the present analysis is to evaluate the relationship among the extant families of odontocetes with the use of the above-stated morphological data. Because it is impossible to know with certainty the anatomy of soft structures of fossil taxa, they are excluded from this analysis directly, but they are commented on in the discussion of certain osteological characters and are used to help determine character polarity. Once a reasonable systematic arrangement of the extant families is completed using all available data, it will be easier for future researchers to integrate the extinct families of odontocetes onto the existing phylogenetic tree(s).

### METHODS

Through examination of a suite of morphological characters, character polarity was determined by outgroup analysis using the Mysticeti and, in some cases, terrestrial mammals as the closest sister-group, and by examination of the paleontological evidence when appropriate. The use of the Mysticeti as a sister-group assumes that the Cetacea are monophyletic. This appears in the literature to be controversial (Rice, 1984). However, an overwhelming amount of morphological (Van Valen, 1968; Barnes and Mitchell, 1978; Fordyce, 1980; Barnes et al., 1985) and cytological (Árnason, 1969, 1974; Árnason et al., 1984; Duffield-Kulu, 1972) data strongly suggest that the mysticetes and odontocetes share a common ancestor. Recent cladistic analyses of sequence data using eye lens proteins (De Jong, 1982) and myoglobin (Goodman et al., 1982) provide additional evidence of cetacean monophyly.

The data were analyzed using the Phylogenetic Analysis Using Parsimony (PAUP, version 2.4.1) program of D.L. Swofford. The coded characters were treated as ordered but unweighted, although the relative weight of individual characters is discussed in the text. The alltrees algorithm was employed and minimum-length Wagner trees were generated.

## CHARACTERS

The following is a discussion of the individual characters used in this analysis, the distribution of each character state throughout the suborder, and the polarity of the character. The numbers for the character states as used in the cladogram (Fig. 39) are listed in parentheses.

### Maxillae Covering Supraorbital Region

(1)—Miller (1923) discussed in detail the telescoping of the cetacean skull and noted that in all odontocetes, the maxillae extend posteriorly, covering the supraorbital region of the frontal bones. This condition is highly modified from the typical mammalian skull plan and is considered to be a derived feature of all odontocetes. The primitive Oligocene odontocete *Agorophius pygmaeus* (Agorophiidae) has a supraorbital region that is incompletely covered by the maxillae but is of the same pattern as all modern odontocetes.

### Single Blowhole

(2)—This character is often listed as a unique feature in all extant odontocetes. As stated previously, in *Physeter catodon* the right and left nasal passages essentially open externally as separate apertures within a common furrow. However, because the two passages become confluent at a deeper level in *Kogia* spp., it is likely that the condition in the more aberrant *Physeter catodon* is a secondarily derived feature. Thus, the single blowhole will be used here as a synapomorphy for the Odontoceti.

### Melon

(3)—This fatty structure is situated in the facial region and rostrum anterior to the nasal passages. It is found in all modern odontocetes, but in *Physeter catodon* its highly modified form is termed the junk (see section on Homology). No terrestrial mammal or mysticete has any structure resembling the melon; therefore, it is considered here a synapomorphy for the Odontoceti.

### Facial Asymmetry

(4)—All extant odontocetes are asymmetrical in that the soft structures on the right side of the facial region are larger and often more highly developed than the structures on the left side. For the reasons discussed in the previous section on facial asymmetry, I think that at least the primitive state of facial asymmetry arose once in the common ancestor of all extant odontocetes and that facial asymmetry is therefore a synapomorphy for the suborder. Cranial asymmetry has been previously suggested to have arisen several times within the odontocetes (Barnes, 1978, 1985a), but this theory is less parsimonious. Barnes's (1978, 1985a) conclusions were based on an evaluation of the cranial asymmetry of fossil taxa, which is somewhat subjective due to the geological processes that can distort fossils.

### Periotic/Tympanic Bulla Attachment to Squamosal

(5, 23, 29)—Most cetaceans have reduced the attachment of the periotic and tympanic bone complex to the skull in correlation with the acoustical isolation of the middle and inner ears from the skull (Fraser and Purves, 1960). There is some confusion as to the terminology for the process that attaches the earbones to the squamosal/exoccipital region of the skull. The terms posterior process (or posterior pedicle) and mastoid process (or pars mastoid) are used almost interchangeably. I will use the term posterior process here because in many advanced odontocetes, the posterior process is so reduced that it does not form any part of the attachment of the mastoid muscles (longissimus capitis, sternocleidomastoideus, spleninus capitis) to the true mastoid process. The decrease in degree of attachment of the posterior process of the periotic to the squamosal was considered by Fraser and Purves (1960) to be the more advanced condition. In addition to outgroup analysis, the paleontological record (Gingerich and Russell, 1981) indicates that the reduced attachment of these bones would seem to be the derived condition, and therefore I agree with Fraser and Purves (1960) on this point. In most terrestrial mammals, the tympanic bulla and petrosal (= periotic in cetaceans) are firmly sutured to the adjacent bones on the posteroventral portion of the skull. In all odontocetes, the periotic and tympanic bulla are loosely sutured to the skull or only attached by small amounts of connective tissue. Several authors (Fraser and Purves, 1960; Kasuya, 1973; de Muzion, 1984) have discussed the reduction in attachment of the earbones to the skull in evolutionary terms. Fraser and Purves (1960) stated that there are three main patterns for the mastoid process in odontocetes: the mastoid fused to the bulla as in *Kogia* spp., the mastoid fused to the squamosal as in *Platanista* spp. and delphinoids, and the mastoid fused to both the tympanic bulla and the squamosal as in ziphiids and *Physeter catodon*. Kasuya (1973) disagreed with Fraser and Purves's interpretation because it was too complex. I also disagree because there is no evidence that the ossification center associated with the mastoid process fuses with the squamosal. After examining skulls from all families of extant cetaceans and one archeocete (LACM VP 24412), I believe that there is an evolutionary reduction in the posterior processes of both the tympanic bulla and periotic. In archeocetes, the tympanic bulla and periotic are fused to each other and this makes it difficult to determine the relative contributions of the tympanic bulla or periotic to the posterior process. The posterior process forms a large discretely formed mastoid process. This mastoid process is wedged between the squamosal and exoccipital and extends distally to the outer lateral edge of the skull. On the outer surface, the mastoid has a rugose or laminar appearance. In mysticetes, the large posterior process is reported by Kasuya (1973) to be formed by relatively equal portions of the periotic and bulla. My examination of the earbones from neonate or fetal mysticetes confirms Kasuya's statement. The posterior process is wedged between the exoccipital and the squamosal in a similar manner as in archeocetes. The external surface of the posterior process does not reach the outer surface of the skull, except in *Caperea* (Fraser and Purves, 1960), and is laminar in appearance. In mysticetes, the periotic also articulates to the braincase by a smaller anterior process. The anterior process of extant odontocetes is extremely reduced and does not articulate with the braincase. In all extant odontocetes, the posterior process of the periotic is extremely reduced. In physeterids and ziphiids, the posterior process of the tympanic bulla is large and reaches the outer surface of the skull. In *Kogia* spp. and ziphiids, this posterior process forms a substantial portion of the combined mastoid and paroccipital processes. In *Platanista* spp., the posterior process of the tympanic bulla is relatively much smaller than in physeterids and ziphiids, but the distal end does reach the outer lateral surface of the skull. In the remaining families Iniidae, Monodontidae, Phocoenidae, and Delphinidae, both the posterior process of the periotic and tympanic bulla are reduced to small prominences and the earbones are held in place primarily by connective tissue. Kleinenberg et al. (1969) and Kasuya (1973) stated that the posterior process of the monodontid *Delphinapterus leucas* was fused to the squamosal. In examining a small series of skulls, I found this not to be true; however, the earbones can be held in place by relatively more connective tissue than found in most delphinoids. Thus, in the reduction of the posterior process of the tympanic bulla, the families Physeteridae and Ziphiidae retain the relatively primitive condition, Platanistidae an intermediate condition, and Iniidae, Monodontidae, Phocoenidae, and Delphinidae exhibit the most derived condition. This interpretation is much more parsimonious than the scenarios presented by previous authors (Fraser and Purves, 1960; Kasuya, 1973; de Muzion, 1984).

### Proximal Sacs (Frontal Sacs/Posterior Nasal Sacs/Inferior Vestibule and Nasofrontal Sacs)

(6, 11, 17, 41)—This complex of nasal diverticula is difficult to interpret in terms of polarity. My interpretation is that the incipient state, which I will term a proximal sac, is present in all modern odontocetes. Three patterns occur: the physeterid condition of a single simple sac off the right nasal passage termed the frontal sac; the ziphiid, platanistid, iniid, monodontid, and phocoenid condition of paired posterior nasofrontal sacs and posterior nasal sacs separated by a transverse fleshy fold and becoming confluent ventrally as the inferior vestibule; and the delphinid condition of paired and well-differentiated nasofrontal sacs and inferior vestibules, but absent or reduced posterior nasal sacs. Although I consider all of these conditions somewhat homologous and derived, the loss of the posterior nasal sac in delphinids is considered to be derived from the morphology found in phocoenids etc.

### Jugal/Lacrimal Fusion

(7)—In all extant platanistids, iniids, monodontids, phocoenids, and delphinids, the lacrimal is fused to the jugal. This fusion is so complete that no suture is typically seen even in fetal skulls. In ziphiids these two bones are quite distinct. In *Physeter catodon* the lacrimal and jugal are tightly appressed to one another and sometimes fused. Little of the lacrimal can be seen because it is deeply wedged between the maxilla and frontal, thus making it difficult to determine the degree of fusion. Flower (1869) stated that the jugal and lacrimal are fused, believing that the large jugal represented both bones. In both species of *Kogia* the jugal is lacking altogether. Because these bones are not fused in mysticetes and terrestrial mammals, the condition found in platanistids, monodontids, phocoenids, iniids, delphinids, and perhaps physeterids is considered derived by outgroup analysis.

### Supracranial Basin

(8)—All extant and fossil sperm whales have a raised facial border that does not include the nasals and premaxillae within a well-formed vertex. From a dorsal view, this feature imparts an amphitheater-like appearance to skulls of physeterids. This structural arrangement is found only in the family Physeteridae and is obviously highly derived. The facial region of the skull of the ziphiid *Hyperoodon* spp. with its raised maxillary crests does approximate this condition; however, the architecture of the well-formed vertex region is distinctly different from that of physeterids.

### Loss of One Nasal Bone

(9)—The skulls of all physeterids lack at least one of the paired nasal bones. Skulls in species of the subfamily Physeterinae lack one nasal bone (Kellogg, 1928). Flower (1869) suggested that it is the right nasal that is lacking in *Physeter catodon*, but did not provide conclusive evidence. Both nasals are lacking in both extant species of *Kogia* (Schulte, 1917) and in the early Pliocene species *Praekogia cedrosensis*.

### Spermaceti Organ

(10)—As stated in the Homology section, this structure is found in all extant physeterids and is not homologous to any structure found in other odontocetes. Therefore, it is synapomorphic for the family Physeteridae.

### Distal Sac

(12)—This diverticulum is found only in physeterids and, as previously discussed, is probably not homologous with the vestibular sac. It is most likely a neomorph unique to physeterids.

### Elongate Mandibular Symphysis

(13)—All extant members of the family Platanistidae, Iniidae and all fossil forms assigned to this group (= Pontoporiidae sensu Barnes, 1985a) have mandibular symphyses that in length exceed over half the length of the entire mandible. This condition is also found in the extinct family Rhabdosteidae (= Eurhinodelphidae) that has an unresolved relationship to other odontocetes (Barnes et al., 1985). Extant and extinct species of the Physeterinae (= Physeteridae sensu Barnes et al., 1985), for which the mandible is known, also have an elongate mandibular symphysis. Both species of *Kogia* have a proportionally shorter mandibular symphysis than *Physeter,* but the posterior shape of the mandibles is similar in that they are Y-shaped. The length of the symphysis portion of the mandibles within the Physeteridae may be a scaling phenomenon with the symphysis length correlating positively with skull length. This would explain why the larger *K. breviceps* has a symphysis that is relatively longer than the smaller species *K. simus.* Thus, it is probable that an elongate mandibular symphysis is a synapomorphy for the Physeterinae, and possibly for the entire family. Other features of the mandibles of physeterids differ from platanistids and iniids. Platanistid and iniid mandibles retain a primitive large coronoid process and a moderately developed angular process. In physeterids both the coronoid and angular processes are extremely reduced, giving the posterior margin of the mandible a rounded appearance in lateral view. The extant delphinid *Steno bredanensis* has a mandibular symphysis that approaches one-third the length of the mandible, whereas most delphinids have a short symphysis. Thus, an elongate mandibular symphysis has undoubtedly evolved in parallel among at least some of these groups, although this character may be synapomorphic within each taxon in that the ancestor to the particular group lacked a long mandibular symphysis. Several genera of archaeocetes are known to have mandibular symphyses that extend posteriorly to about the level of the second premolar. This corresponds to almost half the length of the mandible. Because the origin of this feature is in question, it merits less weight in a phylogenetic analysis.

### Confluence of Nasal Passages

(14)—In all species within the families Delphinidae, Monodontidae, Phocoenidae, Platanistidae, Iniidae, and Ziphiidae, the nasal passages become confluent just distal to the bony nares. In the Physeteridae, the nasal passages remain discrete tubes as far distad as the blowhole or just proximal to the blowhole. Because in both mysticetes and all other mammals, the nasal passages are separate tubes all the way to the external nares, the greater degree of confluence found in non-physeterid odontocetes is considered the derived state for this character.

### Blowhole Ligament

(15)—This connective tissue structure is located at the posterior wall of the narial passages in the odontocete families Platanistidae, Iniidae, Ziphiidae, Monodontidae, Delphinidae, and Phocoenidae. This structure is lacking in all mysticetes and extant species of the family Physeteridae. In ziphiids, *Delphinapterus leucas,* and *Platanista* spp., there is a section of cartilage within the blowhole ligament.

### Premaxillary Sacs

(16)—These diverticula are found within species of the families Ziphiidae, Platanistidae, Iniidae, Delphinidae, Monodontidae, and Phocoenidae. Where present, they are conservative in structure. They are obviously derived because they are lacking in physeterids, mysticetes, and all terrestrial mammals. The slightly distensible pocket that can be felt beneath the left nasal plug of physeterids may be an incipient (or vestigial?) premaxillary sac, but it is certainly not of the same shape as the premaxillary sacs of other odontocetes.

### Enlarged Pterygoid Hamuli

(18)—All ziphiids are noted for the greatly expanded hamulus portion of the pterygoid. This construction of the pterygoid is unique and very conservative in form among modern ziphiids (Fraser and Purves, 1960). The pterygoids of ziphiids and physeterids also differ from all other extant odontocete families in that the lateral lamina is not osseous, but instead consists of a flexible membrane. Due to its widespread occurrence and conservative form among modern ziphiids, one would expect that this would be the condition found in fossil ziphiids. Unfortunately, the fragile nature of the pterygoids does not lend itself to preservation and most fossil odontocetes lack intact pterygoids.

### Enlarged Apical Mandibular Teeth

(19)—Of the extant odontocetes, only ziphiids have an enlarged apical pair of mandibular teeth. In some modern ziphiids however, the apical teeth seem to have moved posteriorly on the mandible (Moore, 1968; Heyning, 1984). This idea, that the more posteriorly positioned enlarged teeth of some species of *Mesoplodon* represent the apical pair, is supported by the fact that vestigial teeth are always found only posterior to the enlarged tooth and never anterior to it (e.g. Fraser, 1953:39). If the more posteriorly positioned teeth were an enlargement of a pair of teeth farther back in the series, one would expect vestigial teeth to be found both anterior and posterior to them. Modifications of the dentition are not unique to ziphiids. The extant species *Monodon monoceros* has the famous enlarged upper apical tooth that may extend 2.5 m in adult males. The extinct delphinoid *Kentriodon pernix* has both upper apical teeth enlarged and projecting forward. Many modern odontocetes have lesser modifications of the teeth that are associated with social interactions (Heyning, 1984). The above discussion serves to illustrate that modification of teeth has evolved several times within the Odontoceti. Although only modern ziphiids have an enlarged apical mandibular pair of teeth, because of the possibility of convergence or parallelism not every fossil found with this condition should be considered a ziphiid without additional characters.

### Elevated Vertex

(20)—This is the raised portion of the skull posterior to the bony nares that includes contributions from the nasals, premaxillae, and maxillae. This elevated vertex is characteristic of all ziphiids to varying degrees. The lowest vertex of any extant ziphiid is that of *Berardius* spp. (Moore, 1968), which is only slightly more elevated than that of some fossil delphinoids of the family Kentriodontidae (Barnes, 1978) and some iniids. However, in both these latter groups, the premaxillae do not contribute significantly to the formation of the vertex. The elevation of the vertex as found in ziphiids is a derived feature.

### Throat Grooves

(21)—All modern ziphiids possess one pair of anteriorly converging throat grooves. Some specimens of *Berardius* spp. have some accessory grooves in addition to the main pair. *Physeter catodon* and *Kogia breviceps* usually have throat grooves, but they are of irregular shape and varying number. Thus, the consistent morphology of the throat grooves found in ziphiids is considered a derived character for the family.

### Temporal Fossa

(22, 33, 35)—The advanced or primitive structure of the temporal fossa is an often-cited character (e.g. Rice, 1984). There are actually several features to this structure that change. For coding purposes, I have divided this structure into two characters. The first is the roofing over of the temporal fossa by the lateral and posterior expansion of the maxillae. This roofing over is clearly the derived state by outgroup analysis and examining the fossils as a directed chronocline. The second character is the reduction in relative size of the zygomatic process of the squamosal. By the same criteria as the first character, reduction of this structure is considered to be the derived condition and I have coded this character in three states depending on the degree of reduction. The primitive condition of a large zygomatic process of the squamosal and a temporal fossa that is not roofed over is found in modern species of the family Platanistidae and Iniidae as well as in the extinct odontocete families Squalodontidae and Agorophiidae, and all archeocetes. In the Ziphiidae, the temporal fossa is roofed over, but the zygomatic process of the squamosal is rather robust with a large exoccipital process. This condition is also found in modern species of the Physeteridae; however, the early Miocene form *Diaphorocetus poucheti* (Kellogg, 1928:fig. 14) has the primitive condition of a large zygomatic process and a temporal fossa that is not roofed over. In the families Monodontidae, Phocoenidae, and Delphinidae, the zygomatic process of the squamosal is either moderately reduced (Monodontidae) or extremely reduced (Delphinidae and Phocoenidae) and all three families possess temporal fossas that are roofed over. Although the large delphinid species *Orcinus orca* does have a substantial zygomatic process, this is considered a secondary development in response to handling larger prey items. The extinct genera *Kampholophus* and *Liolithax* exhibit the primitive construction of the temporal fossa region. These cetaceans were originally considered to be iniids, however Barnes (1978) placed them into the primitive delphinoid family Kentriodontidae. This suggests that the derived condition evolved independently at least within the physeterids and delphinoids. The temporal region of most fossil ziphiids is not known well enough to determine whether the roofing over of the temporal fossa is convergent in this group also.

### Cranial Hiatus

(24)—This feature is an enlarged fontanelle in the region of the periotic bone. Its margins are formed from the squamosal, parietal, and occipital bones (Fraser and Purves, 1960). It is found in all species within the families Iniidae, Monodontidae, Delphinidae, and Phocoenidae, but is weakly formed in the Platanistidae. It is entirely lacking in ziphiids, physeterids, and mysticetes. It is considered derived by outgroup analysis. Some specimens of the delphinid *Stenella coeruleoalba* lack a well-formed hiatus, but this condition is most likely a secondarily evolved feature.

### Air Sinus System

(25, 37)—The region surrounding most of the periotic/tympanic bulla on the ventral aspect of the skull is occupied by an air sinus that extends anteriorly for some distance. Depressions in the skulls of archaeocetes (Kellogg, 1936:107) indicate that they may have had at least the beginning of a pterygoid sinus as well as the peribullary sinus, and the modern mysticetes have relatively simple sinuses of similar construction (Fraser and Purves, 1960). This simple condition of a large undivided pterygoid and peribullary air sac is found in the families Ziphiidae, Monodontidae, and Physeteridae. The condition described for iniids and platanistids by Fraser and Purves (1960) is based on the examination of skulls and radiographs, not on dissections. I dissected the air sinus system of one *Inia geoffrensis* and one *Pontoporia blainvillei*. I found elaborate preorbital and postorbital lobes similar to the derived state found in delphinids. However, the "anterior sinus" of *I. geoffrensis* as indicated on the radiograph of Fraser and Purves (1960) is actually part of the pterygoid sinus medial to the nonosseous lateral lamina of the pterygoid. In delphinids and phocoenids, there are well-formed diverticula off the pterygoid sinus called the preorbital and postorbital lobes. In phocoenids, there is an additional dorsally directed diverticula that extends along the frontal bone and which is considered to be a derived feature.

### Pneumatisized Maxillary Crests

(26)—In *Platanista* spp., the posterolateral edge of the maxillae become expanded and form large crests that overhang the facial fossa. The inside surface is pneumatisized by extensions of the pterygoid air sinuses (Fraser and Purves, 1960; Purves and Pilleri, 1973). This feature is derived.

### Pterygoids Covering Palatines

(27)—In *Platanista* spp., the pterygoids have expanded anteriorly to cover the entire palatine bones. This condition is derived. This condition is also found in the fossil odontocete *Zarachis flagellator* (Kellogg, 1928) and was considered by Kellogg to be related to *Platanista* spp. based on other similarities as well.

### Vestibular Sac

(28, 30, 38)—This diverticulum is discussed in detail in the section on Homology. It is found only in members of the Iniidae, Monodontidae, Delphinidae, and Phocoenidae, and is considered a derived character by outgroup analysis. In phocoenids, the floor of the sac is relatively rigid and is deeply folded. The vestibular sacs of iniids are extremely complex and enlarged on the right side. Both of these features are considered to be uniquely derived from the simpler state as found in delphinids and monodontids.

### Premaxilla/Nasal Contact

(31, 39, 42)—In all extant iniids, the posterior end of the premaxillae are separated laterally from the nasals. In phocoenids, the premaxillae also do not contact the nasals, but this is caused by a shortening of the posterior end of the premaxillae. In many species of extant phocoenids, this reduction of the posterior end of the premaxillae is so extreme that the premaxilla do not border the lateral edge of the bony nares. In delphinids, the posterior end of the left premaxilla is reduced and does not contact the left nasal, but the right premaxilla always is in contact with the right nasal. These features are illustrated and discussed by de Muzion (1984). I consider them all to be derived and of independent origin.

### Widely Separated Pterygoids

(32)—In all species of extant monodontids and phocoenids, the palatal region is broad and flat, and the pterygoids are widely separated laterally by the palatines. This unique palatal structure was first described by Flower (1883) and I have considered it to be derived.

### Facial Plane

(34)—In profile, the rostrum of most odontocetes gradually or abruptly curves upward toward the braincase. Thus, the facial plane is typically slightly to strongly concave. In extant monodontids, the facial plane is either relatively flat (*Monodon monoceros*) or even convex (*Delphinapterus leucas*). I consider this change in the facial plane to be derived in the Monodontidae.

### Premaxillary Bosses or Eminences

(36)—In all fossil and extant species of phocoenids, there are raised rounded bosses on the premaxillae just anterior to the bony nares. Additionally, the premaxillae do not extend posterior beyond the anterior half of the nares. In all other odontocetes, at least one premaxilla extends to the posterior edge of the nares. In both of these characters, phocoenids are derived.

### Spatulate Teeth

(40)—All extant species of phocoenids have spatulate-shaped teeth. This differs from the typical conical-shaped teeth found in all other groups of odontocetes and is considered derived.

## CHARACTERS NOT USED FOR ANALYSIS

The following characters have been used previously in the literature for higher-level odontocete systematics, but I have chosen not to include them, either due to some problem in interpretation for systematic analysis or because they are not pertinent to an analysis at this level.

### Homodont Dentition

This feature is cited as a uniting character for extant odontocetes. The exceptions to this condition are found in some secondarily derived forms such as *Monodon monoceros* with its single tusk, *Inia geoffrensis* and *Lipotes vexillifer* with a slight cingulum on their posterior teeth, and ziphiids that possess at least one enlarged pair of teeth. However, the typical mammalian pattern of heterodonty is found in the extinct odontocete families Squalodontidae and Agorophiidae that have distinctive double-rooted sectorial cheekteeth and procumbent conical anterior teeth. It seems very likely that there is a selective advantage to have simple conical teeth to feed upon fishes, as suggested by Slijper (1962), hence there is a possibility this feature may be parallel in evolutionary development. There is evidence of stomach remains from an archaeocete indicating that fishes were the major prey item (L. Barnes, pers. comm.), and most extant odontocetes feed on fishes at least to some extent. Examination of tooth buds of fetal mysticete whales (Kükenthal, 1893) reveals that they also exhibit homodont dentition. Thus, this feature is either parallel in its evolutionary development or is a synapomorphy for the order Cetacea, not the suborder Odontoceti, and is thus not included in the present analysis.

### Single-rooted Cheekteeth

All extant odontocetes possess teeth that are all single-rooted. Terrestrial mammals and archeocetes have the primitive pattern of multirooted cheekteeth. The extinct primitive odontocete families Squalodontidae and Agorophiidae also had multirooted cheekteeth. It is unclear whether the single-rooted condition evolved in the common ancestor of all modern odontocetes, cetaceans, or whether this feature, like homodont dentition, is a parallel response to strong selection for a better apparatus for catching fish. As above, examination of the tooth buds of fetal mysticetes (Kükenthal, 1893) indicates that they also have single-rooted cheekteeth.

### Rib Articulation

Flower (1869) first mentioned two types of articulation between the posterior ribs and the vertebrae. Rice (1984) summarized the features of the "ziphiid" type of articulation in which the posterior ribs have only capitular attachments to "new" transverse processes, and a "delphinid" articulation in which the transverse processes are situated at an increasingly lower position on the vertebrae posteriorly, with the posterior ribs attached only by their tubercula. Flower (1869) cited the similarity of rib articulation in *Physeter catodon* and *Hyperoodon ampullatus* as a feature that unites the ziphiids and physeterids. In examining the vertebral columns of numerous odontocetes (*Inia geoffrensis, Pontoporia blainvillei, Delphinus delphis, Monodon monoceros, Mesoplodon carlhubbsi, Kogia simus,* and *Physeter catodon*), I found that the previous interpretations are incorrect; in all odontocetes the posterior ribs attach only by the tuberculum to the transverse process. In *Physeter catodon* and ziphiids, the difference is in the manner of change in position of the transverse processes on the vertebrae, being abrupt rather than gradual as in most other odontocetes. The pattern of rib attachment in *Kogia* spp. is exactly like the "delphinid" type and thus the pattern is not even consistent within the Physeteridae. The only exception I found was in *Inia geoffrensis,* in which there is a fusion in the posterior ribs of the capitular and tubercular heads as illustrated by Slijper (1936). Because there is no clear pattern to rib attachment, I will not use it in my analysis.

### Supernumerary Dentition

With the exception of some secondarily derived forms, all odontocetes have dental formulae that far exceed the primitive maximum eutherian number of 48. However, all studies of tooth buds found in the embryos of mysticete cetaceans show that they also exceed the primitive eutherian number (Kükenthal, 1893). Hence, this character may not be synapomorphic for the odontocetes and will not be considered in this analysis. Fordyce (1982) provided evidence that the retention of deciduous teeth alongside the permanent teeth possibly could explain some of the extra teeth; however, he also stated that the number of teeth found in some odontocetes exceeds that which could be explained entirely by this phenomenon.

### Enlarged Mandibular Foramina

This feature is found in all extant odontocetes and in all fossil forms for which the mandible is known. In odontocetes, the enlargement is primarily in a dorsoventral plane, resulting in a laterally narrow elliptical foramen. The ramus posterior of the mandibular foramen, termed the pan region, is thin and laterally convex. In modern mysticetes, the mandibular foramen is slightly enlarged and has a more typical mammalian round or slightly oval shape. However, in fossil mysticetes of the family Cetotheriidae, the mandibular foramen is enlarged in a dorsoventral plane and the pan region is relatively thin, although not as thin as in odontocetes. Thus, in these characters, cetotheres resemble the derived condition found in modern odontocetes. To date, there are no described mandibles attributed to the most primitive mysticete family Aetiocetidae. This dorsoventral enlargement of the mandibular foramen is clearly developed in some archeocetes such as *Basilosaurus cetoides* (Kellogg, 1936:29). This enlargement of the mandibular foramen and thinning of the pan region is clearly a derived feature. Thus, I concur with Barnes and Mitchell (1978) who list the enlarged mandibular foramen as a character uniting mysticetes and odontocetes. If this is true, then the condition found in modern mysticetes must be a reversal. The pan region and enlarged mandibular foramen in modern odontocetes is filled with the intramandibular fat pad. Norris (1964, 1968, 1969) postulated that this region is the primary site of sound reception for odontocetes. Subsequent physiological experiments have provided supporting evidence for this theory (McCormick

**Table 2. Higher-level classification of the modern odontocete families most commonly used today. Note the implied relationship between the families Ziphiidae and Physeteridae. Within the Platanistoidea, the four genera have been variously placed in one to four families.**

- Physeteroidea
  - Physeteridae
  - Ziphiidae
- Platanistoidea
  - Platanistidae
- Delphinoidea
  - Delphinidae
  - Phocoenidae
  - Monodontidae

**Table 3. The second most common classification of the Odontoceti, as used by many authors. This differs from Table 2 in that there is no close relationship implied between the families Ziphiidae and Physeteridae.**

- Physeteroidea
  - Physeteridae
- Ziphioidea
  - Ziphiidae
- Platanistoidea
  - Platanistidae
- Delphinoidea
  - Delphinidae
  - Phocoenidae
  - Monodontidae

**Table 4. Higher-level classification of the extant Odontoceti based on data from facial anatomy and other morphological characters. The superfamilies are listed sequentially within the suborder. When a group name has been changed to a new rank, the author who changed the rank is listed second.**

- Order Cetacea Brisson, 1762
  - Suborder Odontoceti Flower, 1867
    - Superfamily Physeteroidea (Gray, 1821) Gill, 1872
      - Family Physteridae Gray, 1821
        - *Physeter* Linnaeus, 1758
        - *Kogia* Gray, 1846
    - Superfamily Ziphioidea (Gray, 1865) Fraser and Purves, 1960
      - Family Ziphiidae (Gray, 1865)
        - *Tasmacetus* Oliver, 1937
        - *Berardius* Duvernoy, 1851
        - *Ziphius* Cuvier, 1823
        - *Hyperoodon* Lacépède, 1804
        - *Mesoplodon* Gervais, 1850
    - Superfamily Platanistoidea (Gray, 1863) Simpson, 1945
      - Family Platanistidae Gray, 1863
        - *Platanista* Wagler, 1830
    - Superfamily Inioidea (Gray, 1963) de Muzion, 1984
      - Family Iniidae Gray, 1863
        - *Lipotes* Miller, 1918
        - *Inia* D'Orbigny, 1834
        - *Pontoporia* Gray, 1846
    - Superfamily Delphinoidea (Gray, 1821) Flower, 1864
      - Family Monodontidae Gray, 1821
        - *Monodon* Linnaeus, 1758
        - *Delphinapterus* Lacépède, 1804
      - Family Phocoenidae (Gray, 1825) Bravard, 1885
        - *Phocoena* Cuvier, 1817
        - *Australophocoena* Barnes, 1985
        - *Phocoenoides* Andrews, 1911
        - *Neophocaena* Palmer, 1899
      - Family Delphinidae Gray, 1821
        - *Delphinus* Linnaeus, 1758
        - *Stenella* Gray, 1866
        - *Grampus* Gray, 1828
        - *Tursiops* Gervais, 1855
        - *Lagenorhynchus* Gray, 1846
        - *Lagenodelphis* Fraser, 1956
        - *Pepenocephala* Nishiwaki and Norris, 1966
        - *Orcinus* Fitzinger, 1860
        - *Pseudorca* Reinhardt, 1862
        - *Globicephala* Lesson, 1828
        - *Orcaella* Gray, 1866
        - *Feresa* Gray, 1870
        - *Steno* Gray, 1846
        - *Sotalia* Gray, 1866
        - *Lissodelphis* Gloger, 1841
        - *Cephalorhynchus* Gray, 1846

et al., 1980; Bullock and Ridgway, 1972). If the structural change in the cetacean ramus was related to a change in the site of sound reception, then the apparent reversal of this feature in modern mysticetes is even more striking.

## RESULTS AND DISCUSSION

The most frequently used classification for the extant Odontoceti (Table 2) places the families Ziphiidae and Physeteridae in the superfamily Physeteroidea (Simpson, 1945; Kasuya, 1973; Mead, 1975a; de Muzion, 1984) or implied this relationship in a dendrogram (Slijper, 1936). Winge (1942) placed both sperm whales and beaked whales into the same family Physeteridae and separated the two groups into the tribes Physeterini and Xiphiini [sic]. These classifications suggest a common ancestry of beaked whales and sperm whales. A fairly common alternative classification (Table 3) places the ziphiids and physeterids in their own superfamilies (Fraser and Purves, 1960; Barnes et al., 1985). These two classifications differ only with regard to the implied relationship of ziphiids to physeterids; the membership of the other superfamilies is essentially the same in both schemes. The exception to this is the classification by Fraser and Purves (1960), who removed the Monodontidae from the Delphinoidea on the basis of the possession of a more primitive air sac system than that which is found in other delphinoids. Except for the work of de Muzion (1984), the relationship among the superfamilies is not resolved. In a recent paper that utilized electrophoretic data, a dendrogram was presented that listed the Phocoenidae and Ziphiidae as sister-groups

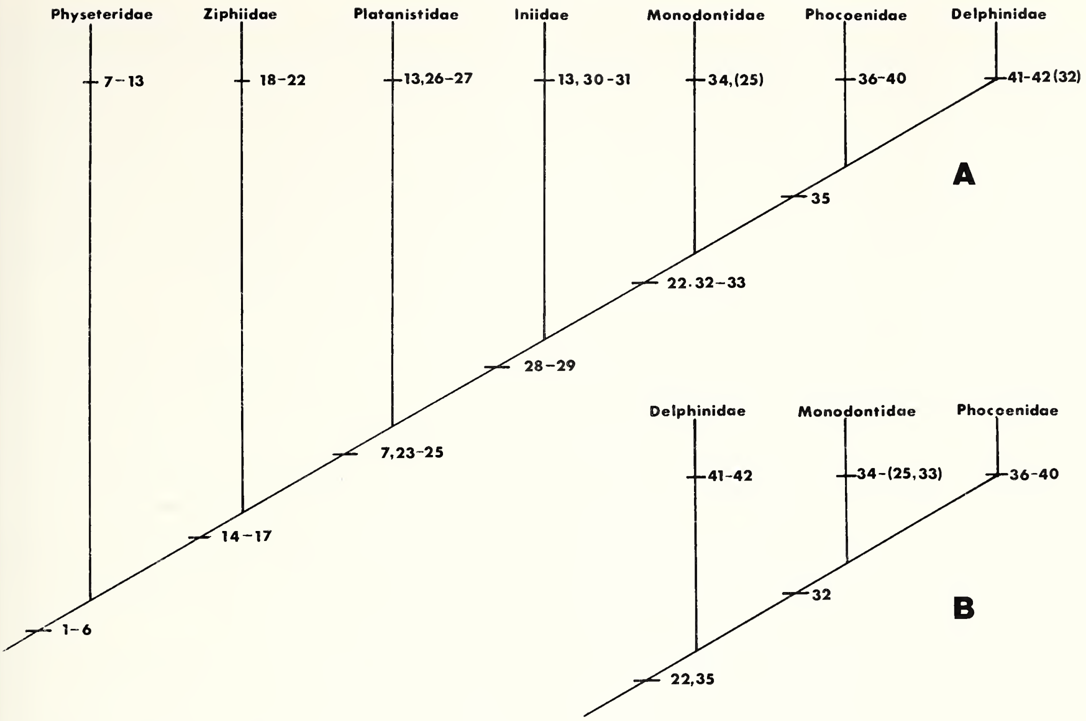


**Figure 39.** Cladogram of the extant families of the Odontoceti based on morphological data. Reversals are noted in parentheses. Synapomorphies used in this analysis are as follows: (1) Maxillae covering supraorbital region. (2) Single blowhole. (3) Development of a melon. (4) Evolution of facial asymmetry. (5) Reduction of the anterior process of the periotic. (6) Development of proximal sacs. (7) Fusion of jugal and lacrimal bones. (8) Evolution of a supracranial basin. (9) Loss of one nasal bone. (10) Development of a spermaceti organ. (11) Proximal sac evolves into frontal sac. (12) Development of a distal sac. (13) Mandibular symphysis becomes elongate. (14) Nasal passages become confluent. (15) Evolution of a blowhole ligament. (16) Development of premaxillary sacs. (17) Proximal sac evolves into inferior vestibule/nasofrontal sac/posterior nasal sac complex. (18) Enlargement of the pterygoid hamuli. (19) Enlargement of the apical mandibular teeth. (20) Elevation of the vertex region that includes the premaxillae. (21) One pair of throat grooves. (22) Temporal fossa becomes roofed over by expansion of the maxillae. (23) Moderate reduction of the posterior process of the tympanic bulla. (24) Development of a cranial hiatus. (25) Elaboration of the pterygoid air sinus to include preorbital and postorbital lobes. (26) Evolution of enlarged pneumatic maxillary crests. (27) The enlarging of the pterygoids that cover the palatines. (28) Evolution of a vestibular sac. (29) Extreme reduction of the posterior process of the tympanic bulla. (30) Hypertrophy of the right side of the vestibular sac. (31) Premaxillae displaced laterally and not in contact with nasals. (32) Pterygoids on palate become widely separated. (33) Zygomatic process of squamosal moderately reduced. (34) Facial plane becomes flat or convex. (35) Extreme reduction of zygomatic process of squamosal. (36) Development of premaxillary bosses. (37) Dorsal intrusion of the air sinus system along the frontal bone. (38) Floor of the vestibular sac becomes rigid and deeply folded. (39) Reduction of posterior edge of premaxillae so they do not form lateral edge of bony nares. (40) Teeth become spatulate in shape. (41) Posterior nasal sac is lost. (42) Posterior end of left premaxilla is reduced and does not contact left nasal.

linked next to the Delphinidae (Shimura and Numachi, 1987). This is contrary to all other published phylogenies. The use of electrophoretic data, especially allozymes, is inappropriate for resolving higher-level systematic relationships (Buth, 1984).

The present phylogenetic analysis resulted in two equally parsimonious cladograms (Fig. 39), with consistency indices of 0.875. Based on the distribution of characters in these two cladograms, I have chosen one preferentially (Fig. 39A). This cladogram provides the basis for a classification using five sequenced superfamilies (Table 4), the Physeteroidea, Ziphioidea, Platanistoidea, Inioidea, and Delphinoidea. The evidence presented here strongly suggests that ziphiids and physeterids do not share a unique common ancestor, and that previous classifications that united these two families did so on the basis of shared primitive characters. Although most researchers have implied a relationship of physeterids to ziphiids, others as far back as Gill (1872) recognized a number of morphological similarities between delphinids and ziphiids.

The suborder Odontoceti is united by six characters in my analysis. Using myoglobin sequence data, Goodman et al. (1982) constructed a phylogenetic tree of the Cetacea that links the mysticetes as the sister-group to the physeterid/ziphiid clade based on three synapomorphic substitutions. McKenna (1987:65) later commented that this "is not a conflict between morphology and molecular biology." I disagree. The six characters that unite the Odontoceti in my analysis are clearly derived and complex anatomical features that include both soft and hard anatomy. In addition, many unique and derived features of the telescoping of the skull are quite different between the two suborders (Miller, 1923). I find it difficult to conceive that the mysticetes would evolve such structures as a single blowhole, melon, etc., and then revert to the primitive state. Alternatively, it is difficult to believe that these features could evolve in parallel. Therefore, based on the number of characters (six-plus vs. three), their structural complexity, and their unambiguous homology, I consider the Odontoceti as a monophyletic assemblage. If I am correct, then the data that Goodman et al. (1982) analyzed contained some homoplasies that obscured the true phylogeny.

Two characters, single-rooted cheekteeth and homodonty, were excluded from my analysis. If these two characters are truly synapomorphic for the Odontoceti, then the extinct families Agorophiidae and Squalodontidae branch off prior to the Physeteridae on the present cladogram.

The Physeteridae is defined by the seven synapomorphies (Fig. 39). The elongate mandibular symphysis found in all species of the Physeterinae may be primitive for the family, and the reduced symphysis found in the Kogiinae may be a reversal. However, the acquisition of an elongate mandibular symphysis has most likely evolved in parallel within one or both families of river dolphins and is one of the homoplasies in the analysis. The fusion of the jugal to the lacrimal is also an apparent homoplasy because it seems to have evolved in parallel in the Iniidae, Platanistidae, and Delphinoidea clade.

There is some argument on how to list the sperm whales. Most classifications list them within one family, the Physeteridae, with two distinct subfamilies, the Physeterinae and the Kogiinae. Barnes et al. (1985) re-elevated these subfamilies to the family level based on "distinctively constructed supracranial basin." This statement seems to me to be vague; there are only small differences between these two groups other than a more complex distal sac and the presence of a sagittal septum in the Kogiinae and allometry differences in the head. Although there is no difference in the branching pattern in either classification, I feel that to raise each subfamily to family status overemphasizes the differences and obscures the relationship of this clade. Most recent classifications have used only one family for all sperm whales and there are no biological grounds to change this classification. In an earlier paper, Barnes (1973) presented many of these same arguments for having only one family for all sperm whales. The oldest known fossil sperm whale, *Diaphorocetus poucheti,* is from Early Miocene rocks in Patagonia.

The remaining odontocete families are united by four synapomorphies and are thus well differentiated from sperm whales. The Ziphiidae is united by five synapomorphies. One character, the roofing over of the temporal fossa, has probably evolved in parallel in the Delphinoidea. The Ziphiidae is a well-defined clade that has a fossil history extending back to the middle Miocene.

The Delphinoidea, Iniidae, and Platanistidae are united by two characters of the ear region: the evolution of a cranial hiatus and the moderate reduction of the posterior process of the tympanic bulla, and the fusion of the lacrimal to the jugal.

An interesting result of this analysis involves the status of the much-disputed superfamily Platanistoidea. The four modern genera of this taxon have been variously classified into one to four families. One recent paper (Zhou, 1982) in which the genera were separated into four different families did so by emphasizing autapomorphies, not examining the pattern of synapomorphies.

Barnes (1985a) placed the modern species *Pontoporia blainvillei, Lipotes vexillifer,* and some fossil taxa into the family Pontoporiidae based on one synapomorphy, the evolution of facial asymmetry. As I have discussed in a previous section, facial asymmetry is unquestionably a synapomorphic character for all extant odontocetes; thus the family Pontoporiidae, as defined by Barnes (1985a), is based on a diagnosis comprised of characters for which the polarity has not been determined. Barnes (1985a) also did not fully discuss why he excluded *Inia geoffrensis,* a species that has been discussed as being related to either *Pontoporia* (Flower, 1867) or *Lipotes* (Miller, 1918; Simpson, 1945). The tooth morphology, including a well-developed cingulum, of both *Lipotes* and *Inia* is almost identical and probably derived. Yet this feature has not been discussed by either Barnes (1985a) or Zhou (1982).

In another recent work, de Muzion (1985) reported evidence that the river dolphins are diphyletic. The cladogram de Muzion (1985) presented is weak because it has far fewer characters than taxa, so that many nodes have no characters and some nodes have the reversal of a character state as a synapomorphy. Thus, the evidence de Muzion marshalled for a diphyletic origin for the platanistids is not convincing. Interestingly, however, the relationship among the living species of river dolphins presented by de Muzion is very similar to the cladogram I present here that also proposes a paraphyletic origin.

Most recent systematic works have not addressed the important question of whether or not the platanistid dolphins are truly holophyletic. The present analysis does shed some light on this particular question. The only synapomorphic feature I could find that seems to unite the Platanistoidea (as conventionally used) is the presence of a long mandibular symphysis, a feature that conceivably evolved in parallel, especially considering that this character apparently is a parallelism in the Physeterinae and represents one of the few homoplasies in the present analysis. It is more probable (and parsimonious) that the platanistoids merely represent a structural grade between the more plesiomorphic ziphiids and physeterids on one hand, and the apomorphic delphinoids on the other hand. By the present analysis, iniids are more derived in that they possess a vestibular sac and have completely reduced the posterior process of the tympanic bulla. The iniids are further united by the unique hypertrophy of the right side of the vestibular sac and the loss of contact between the nasals and premaxillae. The extant genus *Platanista* is thus left in its own monotypic family defined by several apomorphies. This relationship among the extant genera of the "Platanistoidea" is essentially the same as that of Kasuya (1973) based on tympano-periotic morphology and that of de Muzion (1984) based on several morphological features.

A possible alternative phylogeny would be to unite the modern river dolphins by the synapomorphy of an elongate mandibular symphysis and to consider the lack of a vestibular sac in *Platanista* a secondary loss. It is possible that the air-filled maxillary crests of *Platanista* may have replaced at least the hypothesized sound-reflective function of a vestibular sac. If more evidence can be marshalled to support this latter scenario, I believe the extant river dolphins should be divided into two families, the Platanistidae and Iniidae, and both should be placed within the monophyletic superfamily Platanistoidea. Clearly, there is a need to re-examine the systematics of the whole assemblage of river dolphins, both fossil and extant.

I here briefly address the relationships within the Delphinoidea. The general conclusion that this taxon is holophyletic is supported by my analysis, as well as by the fact that previous studies have listed the three currently recognized families as closely as subfamilies within one family. Myoglobin sequence data (Goodman et al., 1982) suggest that the Phocoenidae and Delphinidae are sister-groups; however, there are no data from any monodontid species. Barnes (1978, 1984) separated out two families of fossil delphinoids, the Kentriodontidae and Albireonidae. Known from middle Miocene rocks, the primitive kentriodontid genera *Kampholophos* (Rensberger, 1969) and *Liolithax* (Kellogg, 1955) as defined by Barnes were originally considered to be iniids when they were described. By the present analysis, it is probable that iniids are the closest sister-group to delphinoids and thus the question of the familial relationship of these fossil genera is more understandable. Fossil taxa at the grade level of the iniid/delphinoid split would be difficult to categorize.

The Delphinoidea is the most diverse superfamily of modern cetaceans and is relatively conservative in general morphology, making a clear phylogenetic analysis difficult. The consensus tree generated from both trees of the present analysis created an unresolved trichotomy of the three families within the Delphinoidea. Kasuya (1973) presented a dendrogram of the Odontoceti based on the morphology of the tympano-periotic bone. He analyzed his data phenetically and did not consider fully the amount of variation that might exist within all species. However, Kasuya did present the Delphinoidea as a monophyletic group and united the Phocoenidae and Delphinapteridae (*Delphinapterus* and *Ocaella*) as sister-groups within the superfamily. Fraser and Purves (1960), in their exhaustive review of hearing in cetaceans, provided a classification of the Odontoceti that included the removal of the Monodontidae from the Delphinoidea based on the primitiveness of the air sinus system in monodontids. This feature is one of the homoplasies in the present analysis and one of the reasons I prefer the first cladogram. Thus, I consider the Monodontidae to be the sister-group to the phocoenid/delphinid clade. However, the grouping Delphinoidea in its most common usage can include all three families and still represent a monophyletic assemblage. This is how I define this superfamily. However, I am perplexed as to how such a primitive air sinus system could have evolved within the Monodontidae. Further work is needed to better resolve this problem.

The only extant family within the Delphinoidea that is united by numerous well-defined synapomorphies is the Phocoenidae. Several synapomorphies have been listed for this family (Fig. 39; Barnes, 1985b). However, one derived character, the flattened hard palate with the pterygoids separated broadly by the palatines, is also found in both species of monodontids and to a lesser degree in the species of the delphinid genera *Cephalorhynchus* (Flower, 1883) and *Orcaella*. The condition of the pterygoids coming in contact, or nearly so, is found in all physeterids, ziphiids, platanistids, iniids, and almost all delphinids. I therefore consider that widely separated pterygoids on the palate is a derived feature but one that I believe has evolved independently within the Phocoenidae and Monodontidae.

The Delphinidae is the most species-rich family of modern cetaceans. The Delphinidae is defined by two synapomorphies. Árnason et al. (1984) presented some evidence that a highly repetitive DNA fragment is different in delphinids from the other cetaceans they studied. Many attempts of questionable validity have been made to divide the Delphinidae into subfamilies. The conservative pattern of facial anatomy of the Delphinidae did not allow Mead (1975a) to make substantial statements regarding the systematics of this group based on his data. The tympanic bulla and periotic of *Orcaella* phenetically resemble those of the monodontid *Delphinapterus* more than those of other delphinids and the two were placed in their own family by Kasuya (1973). On the ventral side of the preorbital region of the skull of *Orcaella*, there is extensive excavation of the bone that indicates a well-developed preorbital lobe of the air sinus system. The zygomatic process of the squamosal is also extremely reduced in *Orcaella*. Both of these features are synapomorphies for the delphinid/phocoenid clade and are not found in monodontids. Based on this evidence, I believe that *Orcaella* should be retained in the Delphinidae until more substantial evidence is presented as to why this species should be placed in another family. Preliminary findings using microcomplement fixation indicate a close relationship between *Monodon monoceros* and *Delphinapterus leucas*, but that *Orcaella brevirostris* is more closely related to the other delphinids studied (Lint et al., 1987).

## CONCLUSIONS

Ziphiids have a complex series of diverticula arising from the nasal passage distal to the bony nares. These nasal sacs include the premaxillary sacs and posterior nasal sacs, and nasofrontal sacs with the anterior section of the nasofrontal sacs present in some species; all of which have homologs in the Delphinoidea, Iniidae, and Platanistidae. However, ziphiids lack the vestibular sac that delphinoids and iniids possess. In the more advanced ziphiid genera *Mesoplodon* and *Ziphius*, the posterior section of the nasofrontal sac is reduced or lost entirely.

The melon of ziphiids is quite similar in gross structure to that found in most other odontocetes. In all ziphiid species examined, the melon extends posteriorly into the right nasal plug but not into the left. Fat similar in appearance to that found in the right nasal plug is also found in some specimens on the anterior surface of the right blowhole ligament adjacent to the melon fat within the right nasal plug.

The prenarial basin that forms in the adult males of *Ziphius cavirostris* is filled with the enlarged right nasal plug. This modified plug is composed of very fatty tissue with decreasing amounts of connective tissue anteriorly where it is covered dorsally by a connective tissue sheath. A thin sheet of connective tissue arising from the mesethmoid clearly defines the left- and right-hand structures. Because this structure is located anterior to the nasal passage, it is not homologous to the spermaceti organ found in physeterids as suggested in previous literature, but may be analogous to it.

The architecture of the facial region of physeterids is very different from that found in ziphiids, platanistids, iniids, or delphinoids. The junk region of *Physeter* appears to be homologous with the melon of *Kogia* and other odontocetes. The spermaceti organ found in all physeterids is a neomorphic structure. Physeterids have no diverticula off the left nasal passage, but there is a proximal and a distal diverticulum off the right passage. Due to the extreme difference in structure between physeterids and other odontocetes, it is difficult to determine the homology between the nasal sacs.

A review of the previous literature marshals enough evidence to prove that the facial region is the source of at least most of the sounds produced by odontocetes, including those utilized for echolocation. There is no evidence to support the idea that the larynx is the site of any sound production, and there is positive evidence to disprove that whistles and clicks are produced by the larynx.

The exact mechanism of sound production as theorized for delphinids is not applicable to ziphiids due to the differences in facial anatomy. The lack of a vestibular sac in ziphiids precludes it from functioning as an air reservior or sound reflector. The anatomical evidence suggests that the posterior nasal sacs may, however, serve this function in ziphiids. The structure of the posterior nasal sacs and the orientation of the posterior fibers of the pars anterointernus muscles suggest that air may fill the posterior nasal sac and be forcefully expelled by contraction of the anterointernus muscles, which would cause the blowhole ligament to vibrate. This vibration could be transmitted to the adjacent right nasal plug.

It is suggested that the asymmetry of the facial region of odontocetes represents a primitive feature and has not arisen several times in the evolution of odontocetes as indicated previously by some researchers. This suggestion is based on several lines of evidence. The asymmetry of the facial structures is hypothesized to have resulted from selection for a single sound source. Such a system would avoid potential sound wave interference or cancellation due to two bilateral, but slightly different, sound generators.

A systematic analysis utilizing the data obtained from facial anatomy, as well as other morphological data, strongly suggests that, in the evolution of extant odontocetes, the physeterids diverged first, followed by, in order: the ziphiids, platanistids, iniids, and delphinoids. The common systematic grouping of the Physeteroidea including the Ziphiidae and Physeteridae has been based on primitive features, and thus this taxon is not holophyletic. The modern river dolphins are divided into two cladistically defined families, the Platanistidae and the Iniidae. The most parsimonious phylogeny suggests that the Platanistoidea, as most commonly used, represents a morphological grade between the Ziphiidae and the Delphinoidea. However, it is possible that they could represent a monophyletic grouping. The Delphinoidea is a well-defined taxon that is probably holophyletic. Within this superfamily, the Monodontidae appears to be the sister-group to a delphinid/phocoenid clade. Hopefully with additional morphological data and the increased use of sequence and electrophoretic data, many of the current systematic problems can be more fully resolved.

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# CONTRIBUTIONS IN SCIENCE

## LATE CENOZOIC TAPIRS (MAMMALIA: PERISSODACTYLA) OF WESTERN NORTH AMERICA

GEORGE T. JEFFERSON

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# LATE CENOZOIC TAPIRS (MAMMALIA: PERISSODACTYLA) OF WESTERN NORTH AMERICA

GEORGE T. JEFFERSON[1]

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**ABSTRACT.** Two latest Pliocene and Pleistocene tapir species are recognized from the western United States. *Tapirus merriami* Frick, 1921, is applied to morphologically distinctive, large specimens previously referred to *T. copei* Simpson, 1945, or *T. haysii* Leidy, 1859. *Tapirus merriami* is considered a relatively primitive sister species of *T. haysii. Tapirus merriami* typically is found in the upper Blancan and Irvingtonian of California, is poorly represented in the Rancholabrean of coastal southern California, and has been recovered from uppermost Rancholabrean deposits in Arizona. A smaller tapir, comparable in size to the western species, *T. californicus* Merriam, 1913, or the eastern species, *T. veroensis* Sellards, 1918, is known from the Irvingtonian of northwestern Sonora, Mexico, and the uppermost Irvingtonian of southern Oregon, but typically occurs in Rancholabrean deposits of coastal southern California including Rancho La Brea.

## INTRODUCTION

The recovery of new specimens of *Tapirus* and the discovery of previously unreported materials from the uppermost Pliocene and Pleistocene of southern California, including a dentary from Rancho La Brea, a partial skull from Porter Ranch, and dentary and partial skeleton from the Anza-Borrego Desert, have prompted a review of the fossil tapirs from the western United States (USA) and northwestern Mexico, west of the Rocky Mountains. The late Cenozoic record of tapirs from this region spans late Blancan (latest Pliocene and earliest Pleistocene) through Irvingtonian (early Pleistocene) and Rancholabrean (late Pleistocene).

East of the Rocky Mountains, a large species of tapir is typical of earlier Pleistocene assemblages and a small species of tapir is typical of the Rancholabrean local faunas (Ray and Sanders, 1984). West of the Rocky Mountains, two distinct forms are recognized, which generally reflect the pattern exhibited by the mid-continent and eastern USA records. A large species, typical of late Blancan through Irvingtonian faunas, and a small species, primarily restricted to Rancholabrean faunas, are found along the Pacific coast from southern Oregon to southern California and in northwestern Sonora, Mexico.

The large form, here referred to *Tapirus merriami* Frick, 1921, was previously considered a junior synonym of *T. haysii* Leidy, 1958 (Ray and Sanders, 1984). However, the species can be distinguished from *T. haysii,* including *T. copei* Simpson, 1945 (Ray and Sanders, 1984), by its consistently larger size and primitive, non-molariform $P^2$.

## SUMMARY OF SYSTEMATICS AND NOMINAL SPECIES

Ray and Sanders (1984) discussed the status of the nominal taxa of Pleistocene tapirs from North America and tentatively recognize two groups of species within the genus *Tapirus,* ". . . a smaller late (and probably earlier) Pleistocene form including *T. californicus, T. veroensis, T. tennesseae,* and *T. excelsus;* and a larger, early to middle (and possibly latest) Pleistocene form including *T. haysii, T. merriami* and *T. copei.*" A summary of their review is pertinent to the taxonomic assignment of the western USA specimens. Although cranial materials are required to adequately distinguish tapir species, most taxa unfortunately have been based on isolated teeth.

*Tapirus mastodontoides* Harlan, 1825, was mistakenly based on the deciduous tooth of a mastodon and has been reduced (Ray and Sanders, 1984) to a junior synonym of *Mammut americanum. Tapirus americanus,* used widely in the nineteenth century for both fossils and modern forms, is a junior synonym of extant *T. terrestris.* The trinomial, *T. t. fossilis* Leidy, 1849, apparently was intended to designate a fossil specimen in published faunal lists, not a taxonomic rank below species level (Ray and Sanders, 1984).

*Tapirus haysii* Leidy, 1859, was named from a single $P^4$ from the Neuse River in North Carolina. Simpson (1945) considered the type specimen to be specifically indeterminate. At the same time, he erected *T. copei,* based on a number of upper and lower dentitions and isolated teeth from Port Kennedy, Pennsylvania, which had been previously re-

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[1] George C. Page Museum of La Brea Discoveries, Natural History Museum of Los Angeles County, 5801 Wilshire Boulevard, Los Angeles, California 90036.

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ferred to *T. haysii* by Leidy (1859). However, as Ray and Sanders (1984) stated, the sample upon which Simpson (1945) based *T. copei* was equally inadequate "because skull characters are not available." Ray and Sanders (1984) reinstated *T. haysii,* preferring to retain the original name for this large, typically Irvingtonian, form from the eastern USA.

*Tapirus californicus* Merriam, 1913, was described on the basis of a single lower molar as a small, western USA subspecies of *T. haysii.* Simpson (1945) elevated *T. californicus* to specific rank when he replaced the taxon *T. haysii* with *T. copei.* Contrary to the statements of Lundelius and Slaughter (1976) and Kurten and Anderson (1980), *T. californicus* is significantly smaller that *T. haysii* (including *T. copei*). *Tapirus californicus* is indistinguishable in size from *T. veroensis* Sellards, 1918, which is well represented in the eastern USA. Although *T. veroensis* may eventually prove to be a junior synonym of *T. californicus,* both taxa remain valid pending confirmation from the recovery of more diagnostic specimens (Ray and Sanders, 1984).

Sellards (1918) based *Tapirus veroensis* on a complete skull from Florida. The name has been successfully applied to specimens representing a small form of *Tapirus* found throughout the central and eastern USA. *Tapirus veroensis* has not been adequately distinguished from *T. californicus,* and previous authors have not attempted taxonomic revisions. *Tapirus tennesseae* Hay, 1920, based on isolated teeth, is considered a junior synonym of *T. veroensis* by Ray and Sanders (1984). *Tapirus excelsus* Simpson, 1945, which was based on a juvenile skull, appears to represent *T. veroensis.* Ray and Sanders (1984) prefer to regard *T. excelsus* as a junior synonym of *T. veroensis,* but they do not reject the possibility that it may represent a large subspecies of *T. veroensis.*

The large, Pacific slope species, *Tapirus merriami* Frick, 1921, named from a partial lower dentition, was tentatively reduced to a junior synonym of *T. haysii* by Ray and Sanders (1984). I consider *T. merriami* a valid taxon based on its relatively large size in comparison to *T. haysii* and its consistently distinctive $P^2$.

## WESTERN NORTH AMERICAN SPECIMENS

*Tapirus merriami* is known from only a few localities in California (Fig. 1). The most complete specimen, a skull, dentary and partial axial skeleton, was recently recovered from the upper Blancan Tapiado Wash portion of the Borrego Formation, San Diego County (G.J. Miller, pers. comm., 1986). Isolated post-cranial materials are also known from the upper Blancan or lower Irvingtonian Bautista Beds (Sharp, 1967) and upper Blancan Palm Springs Formation in this area (T. Downs, pers. comm., 1986). The holotype of *T. merriami* (Frick, 1921) was collected from the lower Irvingtonian Bautista Beds (Savage, 1951) in Riverside County. A partial upper dentition, several dentaries with cheek teeth, and numerous isolated upper and lower cheek teeth were also collected by Frick from the lower Irvingtonian (Reynolds and Reeder, 1986) San Timeteo Formation in Riverside County. The uppermost Pliocene/lowest Pleistocene middle member of the Saugus Formation (Saul, 1979) at Porter Ranch in Los Angeles County has yielded a partial skull and dentary of a large tapir now assigned to *T. merriami.* Two partial upper dentitions have been recovered from pre-Rancholabrean deposits, including the Montezuma Formation and other unnamed units, Alameda County (Weaver, 1949). A $P_3$ was collected from the Irvingtonian San Pedro Sand in Orange County.

Rancholabrean deposits in California have produced only three large tapir specimens, a $P^2$ from the La Habra Formation, and a $DP^4$ and an $M^3$ from the Palos Verdes Sand in Orange County (Fig. 2).

All of the late Rancholabrean tapir remains from Arizona represent a large species (Fig. 2). The dentary from Lehner Ranch, Cochise County (Lance, 1959), previously referred to *Tapirus haysii* (Kurten and Anderson, 1980; Ray and Sanders, 1984), is assigned to *T. merriami.* Agenbroad and Downs (1984) referred a large dentary from Shonto, Navajo County, to *T. merriami.* Several large isolated tapir teeth have been recovered from Murray Springs, Cochise County, and fragmentary teeth are known from Ventana Cave, Pima County, Arizona (Colbert, 1950).

All other specimens of *Tapirus* from the western USA and northwestern Mexico (Figs. 1 and 2) are relatively small and closely comparable in size to the western species, *T. californicus* (Merriam, 1913). However, *T. californicus* is, on the basis of available material, indistinguishable from *T. veroensis* (Sellards, 1918) from the eastern USA (see Summary of Systematics and Nominal Species). Most small tapir specimens have been recovered from Rancholabrean, Sangamon, or Wisconsin age deposits west of the California Coast Ranges or from the inland valleys of the central part of California. A single specimen from the uppermost Irvingtonian or lowest Rancholabrean Elk River Formation (Kennedy et al., 1980), near Cape Blanco, Oregon, has been referred to *T. californicus* (Merriam, 1913; Leffler, 1964). A relatively small, Irvingtonian tapir is also known from the El Golfo local fauna from northwestern Sonora, Mexico (Shaw, 1981; Lindsay, 1984). Shaw (1981) has tentatively identified the El Golfo specimens as *Tapirus* sp., cf. *T. veroensis.*

## ABBREVIATIONS

The following abbreviations are used for institutions housing type, referred, figured, and measured specimens: ANSP, Academy of Natural Sciences, Philadelphia; ASM, Arizona State Museum, Tucson; CAS, California Academy of Sciences, San Francisco; F:AM, Frick Collection American Museum of Natural History, New York; IVCM, Imperial Valley College Museum, El Centro; LACM, Natural History Museum of Los Angeles County, Los Angeles; LACM(CIT), Natural History Museum of Los Angeles County, California Institute of Technology Collection; LACMHC, Natural History Museum of Los Angeles County, Hancock Collection, George C. Page Museum; MNA, Museum of Northern Arizona, Flagstaff; RCIC LC, R. Clark Interpretive Center, Los Coyotes, Orange County; SDSNH, San Diego Society of Natural History; UALP, University of Arizona Laboratory of Paleontology, Tucson; UCMP and UCMPV, University of California Museum of Paleontology, Berkeley; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington.

Abbreviations for cheek tooth measurements are: AW, greatest width across anterior loph; L, greatest anterior/posterior length; PW, greatest width across posterior loph; TW, greatest transverse width of $P_2$. All measurements are in millimeters (mm).

## SYSTEMATIC DESCRIPTIONS

Referred specimens are listed in descending order of completeness from skull, upper and lower dentitions through post-cranial materials. Except for recognizing *Tapirus merriami* as a valid species, taxonomy follows Ray and Sanders (1984). All specimens within the size range of *Tapirus californicus* and *T. veroensis* are referred to *T. californicus.* Non-diagnostic specimens and insufficiently described materials that were unavailable for examination are referred to *Tapirus* sp.

### Class MAMMALIA

### Order PERISSODACTYLA

### Suborder CERATOMORPHA Wood, 1937

### Superfamily TAPIROIDEA Gill, 1872

### Family TAPIRIDAE Burnett, 1830

### Genus *Tapirus* Brisson, 1762

### *Tapirus merriami* Frick, 1921

Figures 3–10

*Tapirus merriami* Frick, 1921:311–314, text figs. 26–28.

**HOLOTYPE.** Right dentary fragment with $M_1$ and $M_2$, UCMP 3243/23519.

**EMENDED DIAGNOSIS.** Largest North American member of the genus; much larger than *Tapirus californicus* and *T. veroensis;* as large or larger than *T. haysii;* differs from *T. haysii* (including *T. copei*) in having a sub-molariform (primitive) $P^2$ with a weakly developed protoloph.

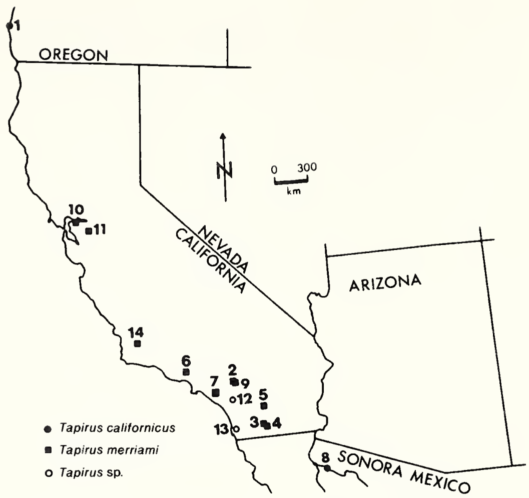

**Figure 1.** Localities for late Blancan and Irvingtonian *Tapirus* specimens from west of the Rocky Mountains. Citations refer to published materials. Formation names are listed where known. Explanation: 1) CAS 101, Cape Blanco, Elk River Formation, Curry County, Oregon (Merriam, 1913; Leffler, 1964); 2) F:AM, El Casco, San Timeteo Formation, Riverside County, California; 3) IVCM 22, 570 and LACM 6654, Vallecito Creek, Palm Springs Formation, San Diego County, California; 4) IVCM 835, Tapiado Wash, Borrego Badlands, Borrego Formation, San Diego County, California; 5) LACM 1186, Coyote Canyon, Bautista Beds, San Diego County, California; 6) LACM 6601, Porter Ranch, Wilbur Wash, Saugus Formation, Los Angeles County, California; 7) RCIC LC 22, Ralph B. Clark Regional Park, San Pedro Sand, Orange County, California; 8) SDSNH 2321, UALP (Borth collection), El Golfo, Sonora, Mexico (Shaw, 1981; Lindsay, 1984); 9) UCMP 3243, Bautista Creek, Bautista Formation, Riverside County, California (includes type of *Tapirus merriami*) (Frick, 1921; Simpson, 1945; Ray and Sanders, 1984); 10) UCMPV 45005, Port Chicago Clay Pit, Montezuma Formation, Alameda County, California; 11) UCMPV 48059, Delta Mendota 20, Alameda County, California; 12) Mann (1955), Santa Gertrudis Creek, Murrieta, Pauba Formation, Riverside County, California; 13) Leffler (1964), San Diego, San Diego Formation, San Diego County, California; 14) N. Rembac (private collection), Horseshoe Spring, Santa Barbara County, California.

**REFERRED MATERIAL.** IVCM 835/3356, skull, partial mandible and partial post-cranial axial skeleton; LACM 6601/16057, posterior portion of skull and fragment of anterior left dentary with partial $P_2$ and $P_{3-4}$; F:AM 17842, right maxilla fragment with $P^2$–$M^3$; UCMPV 45005/38232, right $I^2$, $P^2$ and $M^1$, left $I^{2-3}$, $P^4$ and $M^2$, and right $I_3$; UCMPV 48059/38817, left maxilla fragment with $M^{1-3}$; UALP 7024/17144, left $M^1$ and UALP 7024/17143, $M^2$ (or $M^3$?); LACM 1066/27006, left $DP^4$; F:AM 17844A, left $P^1$; RCIC LC 47/361, left $P^2$; F:AM 17844B, left $M^2$; F:AM 17844C, left $M^3$; LACM 6801/20807, left $M^3$; UALP 7024/17142, left $M^3$; UALP 14/15417, left dentary with $P_3$–$M_3$ (Lance, 1959); MNA 186/23219, right dentary with $P_4$–$M_3$ (Agenbroad and Downs, 1984); F:AM 17840, right

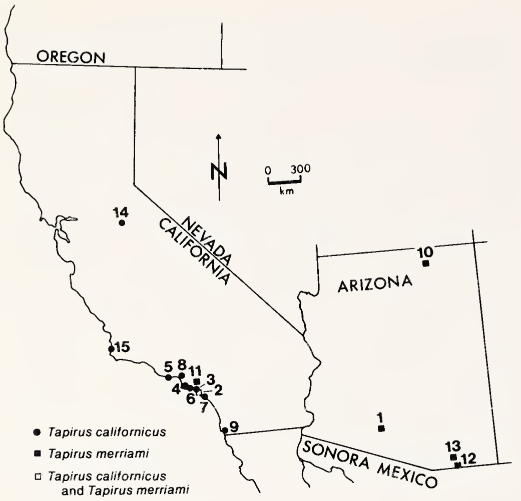

**Figure 2.** Localities for Rancholabrean *Tapirus* specimens from west of the Rocky Mountains. Citations refer to published materials. Formation names are listed where known. Explanation: 1) ASM, Ventana Cave, Pima County, Arizona (Colbert, 1950); 2) LACM 1100, 1066, Newport Bay Mesa (Miller, 1971), LACM 6801, Newport Beach, Palos Verdes Sand, Orange County, California; 3) LACM 1068, Bonita Creek, Orange County, California (Miller, 1971); 4) LACM 1087, Chandler's Sand Pit (Miller, 1971), Stock (1944), San Pedro, Anaheim Boulevard and Vermont Avenue, San Pedro Sand, Los Angeles County, California; 5) LACM 1754, Zuma Creek, Palos Verdes Sand, Los Angeles County, California; 6) LACM 2031, Long Beach near Belmont Pier, Los Angeles County, California (Miller, 1971); 7) LACM 4629, Laguna Nigel, Orange County, California; 8) LACM 5481, Rancho La Brea, Museum Square South (Jefferson, 1986), LACMHC Pit 77, Hancock Park (Harris and Jefferson, 1985), UCMP 3874, Hancock Park (Stock, 1930), Palos Verdes Sand, Los Angeles County, California; 9) LACM(CIT) 594, National City, Bay Point Formation, San Diego County, California (Stock, 1944); 10) MNA 186, Shonto, Navajo County, Arizona (Agenbroad and Downs, 1984); 11) RCIC LC 47, Ralph B. Clark Regional Park, La Habra Formation, Orange County, California; 12) UALP 14, Lehner Ranch, Cochise County, Arizona (Lance, 1959); 13) UALP 7024, Conduits #1 and #4, Murray Springs, Sobaipuri Clay, Cochise County, Arizona (Haynes, 1973; Lindsay and Tessman, 1974); 14) UCMPV 570601, Stony Gulch Cave, UCMPV 65033, Woods Creek near Sonora, Tuolumne County, California (type of *Tapirus californicus*) (Merriam, 1913; Stirton and Weddle, 1929; Simpson, 1945; Ray and Sanders, 1984); 15) UCMPV 65099, Point Sal, Santa Maria, Santa Barbara County, California (Stirton and Weddle, 1929).

dentary fragment with DP$_{2-4}$; F:AM 17844I, right dentary fragment with P$_4$–M$_3$; UCMP 3243/23519 (holotype of *T. merriami*), right dentary fragment with M$_1$ (or M$_2$?) and M$_2$ (or M$_3$?) (Frick, 1921; Simpson, 1945; Ray and Sanders, 1984); RCIC LC 22/86, left P$_3$; F:AM 17847B, right P$_4$; N. Rembac (private collection), right P$_4$; F:AM 17847C, left M$_1$; F:AM 17847A, left M$_2$; F:AM 17846C, left M$_2$(?); F:AM 17844D, left M$_3$; F:AM 17845A, right M$_3$(?); F:AM 17845C, right M$_3$(?); F:AM 17846A, anterior loph of left lower M; F:AM 17846E, anterior loph of left lower M; F:AM 17844K and F:AM 17846B, posterior loph of lower cheek tooth; LACM 6654/20636, left fifth metacarpal; LACM 1186/3284, right fourth metatarsal.

**DISCUSSION.** The holotype (Leidy, 1859) and topotypic specimens (Ray and Sanders, 1984) of *Tapirus haysii* from the Neuse River in North Carolina consist of isolated cheek teeth that represent a large tapir. No cranial materials have been reported. The type specimen of *T. copei,* ANSP 178 (Simpson, 1945) from Port Kennedy, Pennsylvania, considered *T. haysii* by Ray and Sanders (1984), consists of a partial palate with P$^{1-4}$ and the anterior half of M$^1$. ANSP 178 represents a large species, characterized as being relatively advanced dentally with a molariform P$^2$. It has a long diastema that may be an artifact of preservation (Simpson, 1945).

The holotype of *Tapirus merriami* (UCMP 3243/23519) has received considerable attention. Frick (1921) described the specimen from Bautista Creek, California, as a dentary fragment with M$_{1-2}$. This assignment was accepted by Simpson (1945) who considered it larger than and distinct from his *T. copei* as represented by the early Irvingtonian sample from Port Kennedy. Ray and Sanders (1984) referred *T. copei* to *T. haysii.* They questioned Frick's identification, and suggested that the measurements of the teeth (Table 1) better fit the observed size range of M$_{2-3}$ in *T. haysii* (Table 2). Measurements of the holotype exceed the size range of the Port Kennedy specimens in a number of dental parameters and are comparable with the size range exhibited by the topotypic sample of *T. haysii* (Ray and Sanders, 1984) (Tables 1 and 2).

Previously undescribed cranial and dental specimens from the Blancan, Irvingtonian, and Rancholabrean of California that are comparable in size to *Tapirus merriami,* morphologically distinct from and as large or larger than *T. haysii* (including *T. copei*) support the recognition of *T. merriami* as a separate species.

**DESCRIPTION.** The most complete specimen referred to *Tapirus merriami,* IVCM 835/3365 (Figs. 3–5), from the Anza-Borrego Desert, California, consists of an incomplete, dorso-ventrally crushed skull, a partial mandible, and the partially articulated axial hind-quarters of a juvenile individual. Although the basioccipital-basisphenoid suture appears fused, well worn upper and lower DP4's are present, and the second and third molars remain unerupted. The dentition of IVCM 835/3365 is relatively large and lacks the advanced degree of molarization seen on the P$^2$ of *T. haysii* from Port Kennedy (Simpson, 1945). The dental measurements available from this specimen (Table 1) fall within the upper range or exceed those of *T. haysii* (Table 2). Cranial measurements for IVCM 835/3365 are listed in Table 3.

The dorso-lateral profile of the skull of IVCM 835/3365 is not easily reconstructed. The skull appears long and relatively low, a result of post-de-

**Table 1.** Comparative measurements (mm) of western North American specimens referred to *Tapirus merriami*. Explanation: * = measurement approximate/estimate; + = specimen damaged, minimum measurement.

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| F:AM 17840 | | DP$_2$ | | | DP$_3$ | | | DP$_4$ | |
| | L | TW | — | L | AW | PW | L | AW | PW |
| | 31.9 | 17.4 | | 28.3 | 18.9 | 19.0 | 29.0 | 19.0 | 18.4 |
| | | DP$_{2-4}$ | | | | | | | |
| | | L | | | | | | | |
| | | 85.9 | | | | | | | |
| F:AM 17841 | | P$_4$ | | | M$_1$ | | | | |
| | L | AW | PW | L | AW | PW | | | |
| | 27.4+ | 22.7 | 23.4 | · | · | 20.1 | | | |
| | | M$_2$ | | | M$_3$ | | | P$_4$–M$_3$ | |
| | L | AW | PW | L | AW | PW | | L | |
| | · | · | 22.6* | 33.9 | 23.9 | 21.6 | | 115.7 | |
| F:AM 17842 | | P$^4$ | | | M$^1$ | | | M$^2$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 28.5+ | · | · | 32.4+ | 32.9 | · | 33.2+ | · | · |
| | | P$^1$–M$^3$ | | | | | | | |
| | | L | | | | | | | |
| | | 185* | | | | | | | |
| F:AM 17844A | | P$^1$ | | | | | | | |
| | L | TW | — | | | | | | |
| | 22.4 | 20.6 | | | | | | | |
| F:AM 17844B | | M$^2$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 30.6 | 34.8 | 30.6 | | | | | | |
| F:AM 17844C | | M$^3$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 29.7 | 37.6 | 29.8 | | | | | | |
| F:AM 17844D | | M$_3$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 37.4 | 29.8* | 27.1 | | | | | | |
| F:AM 17845A | | M$_3$(?) | | | | | | | |
| | L | AW | PW | | | | | | |
| | 31.3 | 22.3 | 17.8 | | | | | | |
| F:AM 17845C | | M$_3$(?) | | | | | | | |
| | L | AW | PW | | | | | | |
| | 32.0 | 23.7 | 21.8 | | | | | | |
| F:AM 17846C | | M$_2$(?) | | | | | | | |
| | L | AW | PW | | | | | | |
| | 32.2 | 23.4 | 22.7 | | | | | | |
| F:AM 17847A | | M$_2$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 30.0+ | 22.1 | 19.9 | | | | | | |
| F:AM 17847B | | P$_4$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 30.1 | 23.3 | 21.6 | | | | | | |

Table 1. Continued.

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| F:AM 17847C | | $M_1$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 26.2+ | 22.4 | 19.4 | | | | | | |
| IVCM 3356 | | $DP^4$ | | | $P^2$ | | | $P^3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 23.1 | 26.9 | 25.9* | 22.4 | · | · | · | · | · |
| | | $M^1$ | | | $M^2$ | | | | |
| | L | AW | PW | L | AW | PW | | | |
| | 26.1 | 26.5 | 23.7 | 25+ | 30.5+ | · | | | |
| | | $DP_4$ | | | $P_2$ | | | $P_3$ | |
| | L | AW | PW | L | TW | — | L | AW | PW |
| | 25.6+ | 18+ | · | 27.9 | 17.5 | | 27.3 | 17.2 | 18.4 |
| | | $M_1$ | | | $P_2$–$M_1$ | | | | |
| | L | AW | PW | | L | | | | |
| | · | 20.5 | · | | 107* | | | | |
| LACM 16057 | | $P_2$ | | | $P_3$ | | | $P_4$ | |
| | L | TW | — | L | AW | PW | L | AW | PW |
| | 28.4 | 17.7* | | 26.7 | 19.1 | 21.9 | · | 21.5 | · |
| LACM 20807 | | $M^3$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 28.9 | 32.6 | 28.5 | | | | | | |
| LACM 27006 | | $DP^4$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 26.2 | 25.3 | 27+ | | | | | | |
| MNA 23219 | | $DP_4$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 24.2 | 24.2* | 25.2 | | | | | | |
| | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 24.4 | 23.4 | 21.9 | 31.1 | 24.7* | 24.7 | 34.2 | 26.0 | 23.1 |
| RCIC LC 361 | | $P^2$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 25.7 | 26.6 | 27.0 | | | | | | |
| RCIC LC 86 | | $P_3$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 25+ | 20.3 | · | | | | | | |
| UALP 15417 | | $P_2$ | | | $P_3$ | | | $P_4$ | |
| | L | TW | — | L | AW | PW | L | AW | PW |
| | 26.7 | 17.9 | | 26.7* | 16.8* | 21.4 | 29.7 | 20.4 | 20.7* |
| | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 25.4 | 20.8 | 20.6 | 30.6* | 22.6* | 22.3* | 33.7 | 24.2 | 21.1 |
| UALP 17144 | | $M_1$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 26.6 | · | · | | | | | | |

Table 1. Continued.

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| UALP 17143 | | $M_2$ (?3) | | | | | | | |
| | L | AW | PW | | | | | | |
| | 30.8 | · | · | | | | | | |
| UALP 17144 | | $M_3$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 31.8 | · | · | | | | | | |
| UCMPV 23519 | | $M_1$ (?2) | | | $M_2$ (?3) | | | | |
| | L | AW | PW | L | AW | PW | | | |
| | 32.5* | 23.7 | 22 | 32.5 | 23.6 | 20.5 | | | |
| UCMPV 38232 | | $P^3$ | | | $P^4$ | | | | |
| | L | AW | PW | L | AW | PW | | | |
| | 24.5 | 26.5 | 29.8 | 26.5 | 27+ | · | | | |
| | | $M^1$ | | | $M^2$ | | | | |
| | L | AW | PW | L | AW | PW | | | |
| | 27.0 | 33.1 | 32.8 | 30.9 | 35.1 | 31.0 | | | |
| UCMPV 38817 | | $M^1$ | | | $M^2$ | | | $M^3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 25.0 | 27.5* | 31* | 28.2 | 23.5* | 29.5* | 30.0* | 34.5* | 28+ |
| Rembac | | $P_3$ (?4) | | | | | | | |
| | L | AW | PW | | | | | | |
| | 26.1 | 20.2 | 21.8 | | | | | | |

positional crushing. The upper contour of the temporal crests and the frontals appear to have been relatively straight.

Only the anterior portions of the temporal crests are preserved. They are low and divide anteriorly and posteriorly. The median, intertemporal table between the paired crests is relatively narrow (a minimum of approximately 11 mm) given the dental age of the individual. Along the side of the cranium, the temporal-parietal suture is not fused and trends roughly horizontally in lateral view. The parietals are not coossified in the sagittal plane. Most of the postero-dorsal surface of the cranium is missing and there is no evidence of an interparietal bone. The posteriorly divergent temporal crests delineate a triangular area that measures about 80 mm in length and 40 mm in transverse width along its posterior margin above the occipital plate. The lambdoid crests are very well developed, and flare laterally and posteriorly, projecting 60 mm beyond the posterior extent of the occipital condyles. However, several tens of millimeters of this dimension may be an artifact of dorso-ventral crushing.

The auditory meatus is rounded and open ventrally. The postero-lateral margin of the postglenoid and the antero-lateral margins of the mastoid processes converge ventrally from a separation of 11 to 8 mm. The right petrosal is missing and the left is obscured by matrix.

The antero-lateral portion of the spiral groove/channel for the dorso-lateral nasal diverticulum is preserved in the supraorbital flange of the right frontal. Here, the groove is shallow and approximately 3 mm in transverse width. The groove is relatively narrow and deep adjacent to the postero-dorsal edge of the maxilla. The anterior portion of the groove curves laterally and ventrally around, and 14.5 mm anterior to, the anterior edge of the orbit. The shape and position of the lacrimal is not apparent. An isolated nasal fragment is preserved, but its location relative to the fragmentary and incomplete frontals is not evident. The medial portion of the maxilla and a dorsal flange for the mesethmoid cartilage is not preserved.

Although the premaxillae are relatively complete, only the root of the right $I^3$ is preserved. A small right upper canine (7 mm long) is present at the premaxilla/maxilla suture 49 mm anterior to the anterior root of the $P^1$. This sharply pointed, conical tooth is virtually unworn and curves gently lingually. The posterior, ascending portions of the premaxillae are approximately 100 mm long, postero-dorsal to the inter-premaxillary suture. The premaxillae taper to a rounded point above the anterior edge of $P^1$. The dorsal surfaces of the premaxillae exhibit a shallow, linear depression parallel to the medial border.

The crowns of the right and left $P^1$ and the right $P^2$ are missing. Only the antero-lingual portion of the left $P^2$ is preserved. In contrast to the advanced degree of molarization described by Simpson (1945) in his diagnosis of *Tapirus copei,* the protoloph on

**Table 2. Comparative measurements (mm) and observed size range of cheek teeth of *Tapirus haysii* from the central and eastern United States.**

***Tapirus haysii***
**Banners Estate, Neuse River, North Carolina**
**Holotype (measurements from Leidy, 1859)**

| | L | AW | PW |
|---|---|---|---|
| ANSP 11504 $P_4$ | **26.3** | **21.2** | **21.6** |

**Topotypic specimens**
**(measurements from Ray and Sanders, 1984)**

| | L | AW | PW |
|---|---|---|---|
| USNM 215062 $M^2$ or $M^3$ | 28.9 | 34.1 | 30.1 |
| USNM 215202 $M^3$ | 28.6 | 33.5 | 30.4 |
| USNM 34270 $M_2$ | 29.8 | 24.3 | 23.0 |
| USNM 243692 $M_2$ | 33.3 | 25.1 | 23.0 |
| USNM 215061 $M_3$ | 33.2 | 24.0 | 21.4 |

***Tapirus haysii* (*T. copei*)**
**Port Kennedy, Pennsylvania**
**(measurements from Simpson, 1945)**

| | L | AW | PW |
|---|---|---|---|
| $P^1$ | 22.4–24.9 | TW 19.6–21.5 | — |
| $P^2$ | 21.9–24.0 | 25.5–26.5 | 27.4–27.9 |
| $P^3$ | 22.7–24.5 | 27.0–29.5 | 26.1–29.0 |
| $P^4$ | 24.1–26.4 | 29.9–31.8 | 28.4–30.1 |
| $M^1$ | 25.8–26.4 | 28.9–31.1 | 25.8–27.9 |
| $M^2$ | 27.3–29.7 | 31.3–34.9 | 28.0–31.5 |
| $M^3$ | 26.8–29.2 | 31.0–34.1 | 26.5–29.0 |
| $P_2$ | 24.7–27.0 | TW 15.5–17.6 | — |
| $P_3$ | 23.0–25.1 | 16.1–18.0 | 17.8–20.1 |
| $P_4$ | 24.1–24.9 | 18.3–21.7 | 19.5–22.8 |
| $M_1$ | 23.4–27.0 | 19.8–22.9 | 18.7–20.8 |
| $M_2$ | 27.4–30.8 | 20.5–24.1 | 18.3–22.8 |
| $M_3$ | 30.1–31.1 | 21.7–23.8 | 19.2–20.5 |

the left $P^2$ is not fully developed. A well developed protoloph, which joins with the antero-lingual side of the paracone, is present in the Port Kennedy tapir (Simpson, 1945:67, fig. 10A). In IVCM 835/3365, this feature is expressed as a weak ridge that extends lingually from the postero-lingual side of the parastyle toward the position of the protocone in a complete tooth. This condition is also present in RCIC LC 47/361 and UCMPV 45004/38232 (Figs. 9 and 10). The lingual margin of this moderately worn $P^2$ is missing, precluding transverse measurements. The right and left $P^3$ are present but very fragmentary and not measurable.

The enamel crowns of both $DP^4$'s have been completely removed through occlusal wear, and the dentine core of these teeth is cupped or concave. Interdental wear (abrasion on the contact surfaces between the anterior and posterior edges of adjacent teeth that results in interdental pressure facets) has removed at least 1.5 mm from the total length of the $DP^4$'s (Table 1).

Both $M^1$'s exhibit moderate occlusal wear and the $M^2$'s are partially erupted above the alveolar borders but unworn. The $M^3$'s have not erupted and are not visible.

The left $I_{1-2}$ and right $I_2$ are present in the fragmentary mandibular symphysis. The ascending ramus of the left dentary and much of the posterior portion of the right dentary are missing. Only the $P_2$ is preserved on the right side. This tooth is considerably more worn than the left $P_2$, suggesting malocclusion with the right $P^1$. In the left dentary, $P_{2-3}$ show slight occlusal wear, the $DP_4$ is worn flat but not cupped, the $M_1$ is moderately worn, and the $M_2$ has not erupted above the alveolar border. This cheek tooth series exhibits no interdental wear.

Post-cranial axial elements from IVCM 835/3365 include an atlas fragment, the last three thoracic vertebrae and a complete lumbar and sacral vertebral series. The right and left XII and XIII ribs and both innominates were found partially articulated with the thoracic and sacral vertebrae. First and second phalanges of this individual were also recovered.

The numerous specimens collected by Frick from El Casco, Riverside County, California, represent a large tapir, comparable in size to *Tapirus merriami* (Table 1). The partial right maxilla (F:AM 17842) contains the roots of $P^{1-3}$ and well worn crowns of $P^4$–$M^3$. In this specimen, the anterior palatine foramen is located medial to the posterior margin of the $P^4$. The length of the maxillary suture along the mid-line of the palate is 115 mm. Although the crowns of $P^4$–$M^2$ have been completely removed and all teeth exhibit interdental wear, dental measurements of F:AM 17842 exceed those of the topotype of *T. haysii* (Ray and Sanders, 1984) (Tables 1 and 2). F:AM 17841, a right dentary fragment with $P_4$, partial $M_{1-2}$ and $M_3$, represents an old individual which also exceeds the observed size range of the tapir from Port Kennedy. It is comparable with the largest topotypic specimens of *T. haysii*. A well preserved, large juvenile right dentary fragment with $DP_{2-4}$ in slight wear was also recovered from El Casco (Fig. 6). Other isolated upper and lower cheek teeth are as large or larger than those in the sample of *T. haysii* from Port Kennedy, Pennsylvania (Tables 1 and 2).

Although the partial cranium from Porter Ranch, California (LACM 6601/16057) (Fig. 7), lacks the anterior portion of the skull, measurements on the inferior dentition (Fig. 8; Table 1) indicate that it represents a large tapir. The size of these teeth is slightly greater than the observed range of *Tapirus haysii* (Table 2) reported by Simpson (1945) from Port Kennedy. Diastema length from lower C to $P_2$ measures 55.2 mm.

The posterior portion of the skull is severely

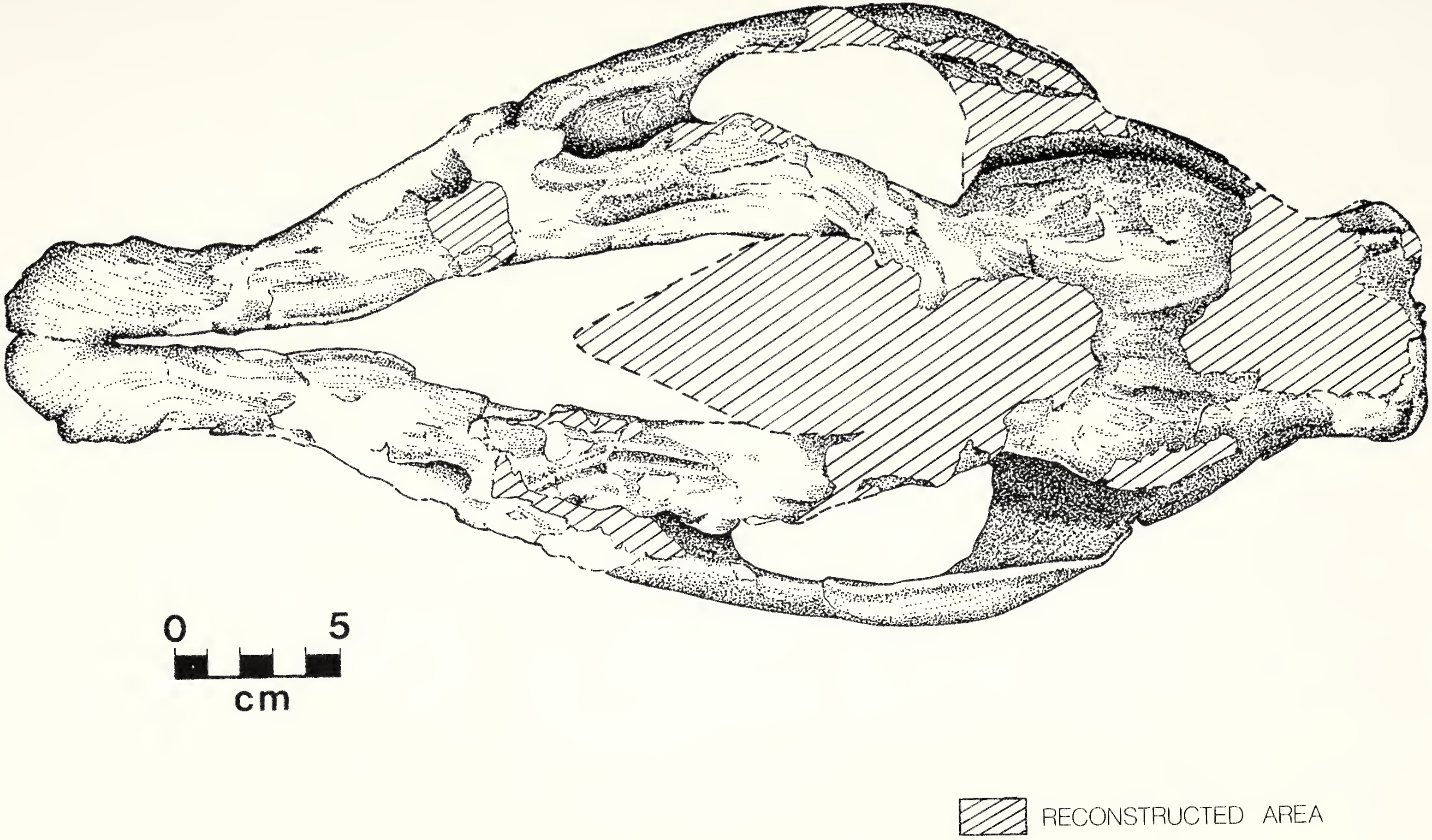

Figure 3. *Tapirus merriami,* dorsal view of skull IVCM 835/3365.

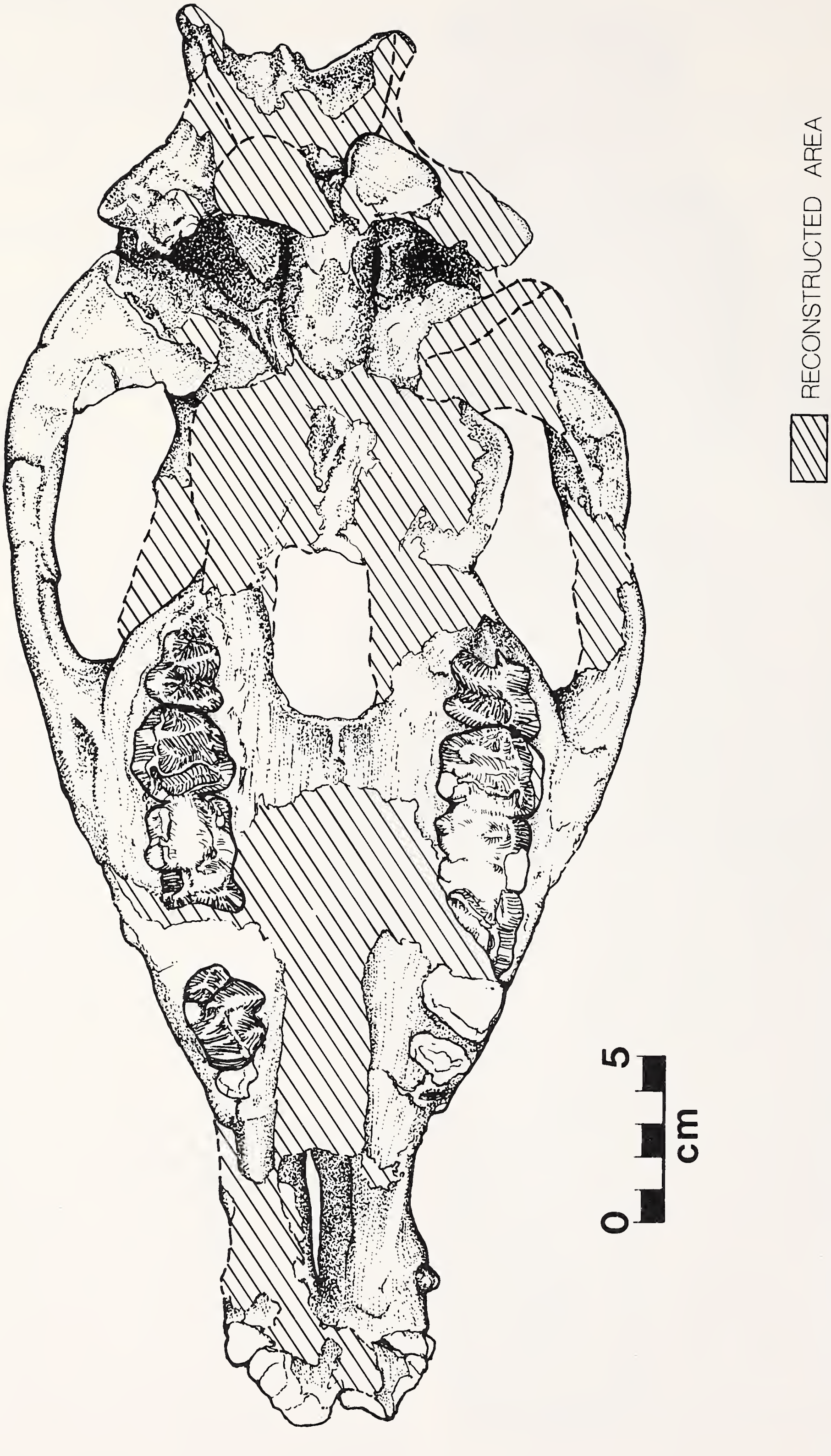

**Figure 4.** *Tapirus merriami*, ventral view of skull IVCM 835/3365.

damaged and appears to have been abraded by stream transport. However, some osteological observations and measurements are possible. The parietals are fully coossified in the saggital plane. The temporal crests on the parietals are low and the median, intertemporal table between the crests is relatively narrow (approximately 14.5 mm). The crests diverge posteriorly, bordering a weakly rugose, flat triangular area that is about 51 mm in length and 47 mm in transverse width above the occipital plate. An interparietal bone is not present. Height of the occipital plate above the dorsal edge of the foramen magnum is about 86 mm. The greatest transverse distance from the center of the foramen magnum to the lateral edge of the right occipital condyle is 38.5 mm, or an occipital condylar breadth of 77 mm. Maximum breadth of the lambdoidal crests is estimated at greater than 72 mm. These crests do not project posteriorly beyond the occipital condyles as in IVCM 835/3365. The temporal-parietal suture is straight, crosses the middle of the cranium, and has a slight antero-ventral dip. The trace of this suture is marked by a zone of foramina and smooth pits. Transverse width across the basicranium measured to the postero-lateral margins of the glenoid fossae is slightly greater than 180 mm. The postero-lateral margin of the postglenoid and the antero-lateral margin of the mastoid processes are parallel and widely separated (21 mm). The auditory meatus is rounded and ventrally open, presenting an inverted U-shape in lateral aspect. Both petrosals are present, and contained the incudes and mallei.

The partial upper dentition (UCMPV 45005/38232) from Alameda County, California, represents a mature individual with the $M^2$ in slight wear and showing only a small amount of interdental wear. The tooth is large (Table 1) and exceeds the upper size range of *Tapirus haysii* (Table 2) from Port Kennedy and the topotypic specimens from North Carolina (Ray and Sanders, 1984). Although the right $P^2$ exhibits moderate wear, the protoloph is weak and not fully developed. It connects the protocone with the postero-lingual side of the parastyle (Fig. 9), not with the paracone as in the Port Kennedy tapir. This character is similar to the condition in IVCM 835/3365 and RCIC LC 47/361.

UCMPV 48059/38817, a left maxilla fragment with $M^{1-3}$ also from Alameda County, represents a very mature individual with well worn teeth. All of the enamel crown of $M^1$ and most of the enamel crown of $M^2$ has been removed. Interdental wear is evident on all teeth. Approximately 1.5 mm has been worn from the anterior and posterior margins of the $M^1$. The anterior margin of the $M^2$ shows slight interdental wear and the anterior margin of the $M^3$ exhibits approximately 1 mm of wear. Nevertheless, the size of the specimen (Table 1) is large in comparison to those in the Port Kennedy sample and the topotype of *T. haysii* (Ray and Sanders, 1984) (Table 2).

The upper molars from Murray Springs, Arizona,

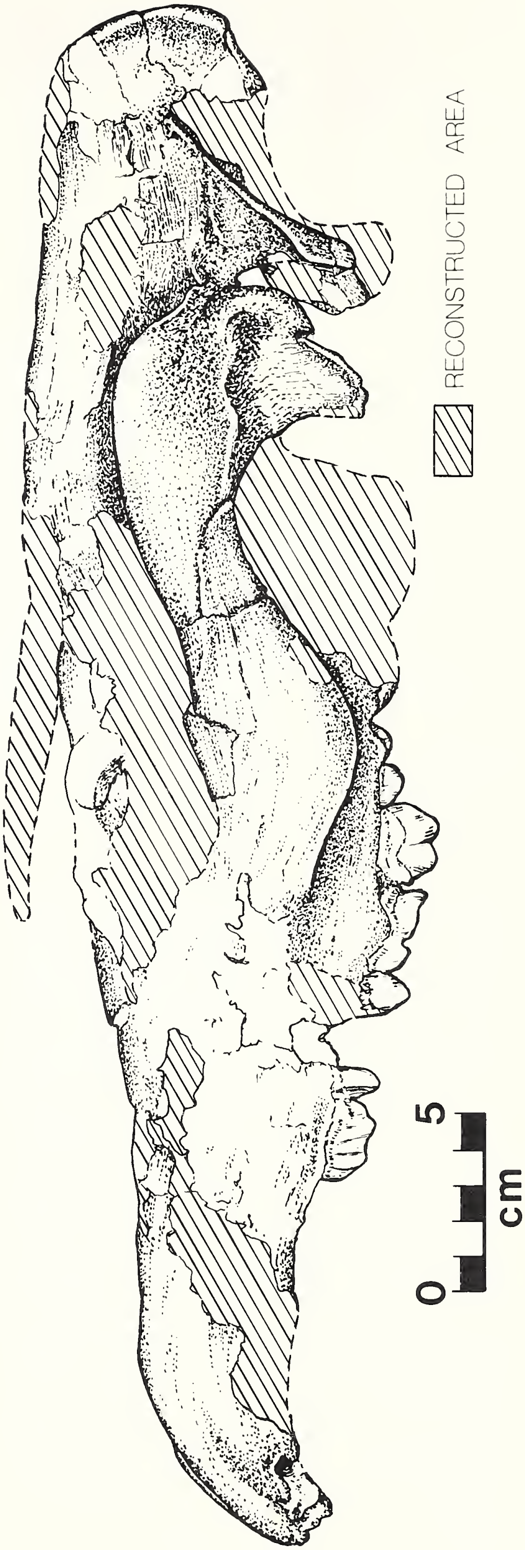

**Figure 5.** *Tapirus merriami*, left lateral view of skull IVCM 835/3365.

**Table 3. Cranial measurements (mm) of *Tapirus merriami* IVCM 835/3356. Measurements follow von den Dreisch (1976). The specimen is crushed and incomplete precluding some standard cranial measurements. The position of the prosthion is estimated ± 1 mm. Explanation: * = measurement approximate/estimate; + = specimen damaged, minimum measurement.**

| Measurement | Value |
|---|---|
| Length akrocranion to prosthion | 225+ |
| Length basion to prosthion | 355* |
| Length nasion to prosthion | 272* |
| Length oral border orbits to prosthion | 178* |
| Length staphylion to prosthion | 199* |
| Length cheek tooth row | 115 |
| Breadth otion to otion | 128 |
| Breadth occipital condyles | 70 |
| Breadth euryon to euryon | 116* |
| Breadth zygion to zygion | 187 |
| Breadth postorbital constriction | 72 |
| Breadth ectorbitale to ectorbitale | 118* |
| Breadth entorbitale to entorbitale | 101 |
| Breadth skull at posterior edge $M^1$ | 166 |
| Depth skull, occipital crest to anterior margin basioccipital | 132 |
| Greatest palatal breadth | 111 |
| Palatal breadth at posterior edge $P^1$ | 76 |
| Length C–$P^1$ diastema | 49 |
| Length nasal opening | 147* |
| Breadth nasal opening at supraorbital processes | 55 |
| Length anterior margin nasal opening to prosthion | 118 |
| Breadth lateral flare lambdoidal crests | 73 |

appear to represent two large individuals, $M_{1-2}$ ($M_{2-3}$?) (UALP 17143 and 17144) and an isolated $M^3$ (UALP 17142). Only length measurements were possible on the three unworn but very fragmentary teeth (Table 1). However, in this dimension the specimens exceed the size range of the Port Kennedy sample of *Tapirus haysii.* Contrary to the statement of Agenbroad and Downs (1984), post-cranial tapir materials are not known from Murray Springs, Arizona (J. Saunders, pers. comm., 1986).

RCIC LC 47/361, a single left $P^2$ (Fig. 10) from the La Habra Formation in R. Clark Regional Park, Orange County, California, represents a young adult with only slight occlusal wear. As with the $P^2$ in IVCM 835/3356 and UCMPV 45004/38232, a weak ridge connects the protocone with the postero-lingual side of the parastyle. This is in contrast to the diagnosis by Simpson (1945) of the $P^2$ in *Tapirus copei.* The dimensions of the tooth (Table 1) are large in comparison to the Port Kennedy sample (Table 2). The transverse width of the partial left $P_3$ from the San Pedro Sand in R. Clark Regional Park, RCIC LC 22/86, is also large in comparison to *T. haysii.*

The left $DP^4$ (LACM 1066/27006) from the Palos Verdes Sand at Newport Bay Mesa, California, lacks preserved roots and, although occlusal wear is slight, exhibits only half the crown height of permanent premolars in *Tapirus haysii.* Like the $P^4$, both anterior and posterior lophs are well developed and connect with the ectoloph. It is larger than IVCM 835/3356 and considerably larger than the dimensions reported by Ray and Sanders (1984: 294, table 1) for a $DP^4$ (with associated skull and dentition) from Claiborn Cave, Tennessee (Bogan et al., 1980), which was referred to *T. veroensis.*

The $M^3$ (LACM 6801/20807) from Newport Beach, California, is well rooted but unworn. Dimensions (Table 1) of this specimen fall within the size range of *Tapirus haysii* from Port Kennedy.

The two dentaries, UALP 14/15417 (Lance, 1959) from Lehner Ranch and MNA 186/23219 from Shonto, Arizona (Agenbroad and Downs, 1984), both represent very large individuals (Table 1). They exceed the size range of *Tapirus haysii* from Port Kennedy (Table 2) and approach or exceed the size of the type of *T. merriami* from Bautista Creek in a number of dental parameters (Table 1) (Agenbroad and Downs, 1984).

A single right $P_3$ or $P_4$ was recently recovered by N. Rembac (pers. comm., 1987) from questionable Pleistocene deposits near Horseshoe Springs in the San Rafael Mountains, Santa Barbara County, California. The age of these deposits is not known, and the location is tentatively plotted with other pre-Rancholabrean specimens on Figure 1. The specimen exhibits moderate occlusal wear and a total of approximately 1 mm of interdental wear on the anterior and posterior margins of the crown. It is comparable in size to the $P_3$ in LACM 16057 (Table 1).

The isolated, post-cranial materials from the Anza-Borrego Desert are tentatively identified as *Tapirus merriami.* These include a fifth metacarpal, LACM 6654/20636, length 110.1 mm, transverse width of proximal articulation 20.2 mm, and a fourth metatarsal, LACM 1186/3284, length 121.2 mm, transverse width of proximal articulation 25.0 mm.

## *Tapirus californicus* Merriam, 1913

Figure 11

*Tapirus haysii californicus* Merriam, 1913:169–172, text fig. 1.

**HOLOTYPE.** Left $M_2$, UCMP V65033/8747.

**EMENDED DIAGNOSIS.** Small North American member of the genus; the size of *Tapirus veroensis;* smaller than *T. haysii* (including *T. copei*) and *T. merriami* (Fig. 12). Dental morphology not separable from *T. veroensis.*

**REFERRED MATERIAL.** LACM 1087/125981 (cast from Cabrillo Beach Museum collection, San Pedro, California), partial left maxilla with $P^2$–$M^2$ and anterior $M^3$; CAS 101, right maxilla fragment with $M^{1-3}$ (Merriam, 1913; Leffler, 1964); F:AM 17844E, right $P^1$; left $P^4$ (no specimen or locality number given, Stock, 1944); F:AM 17846D, left $M^1$;

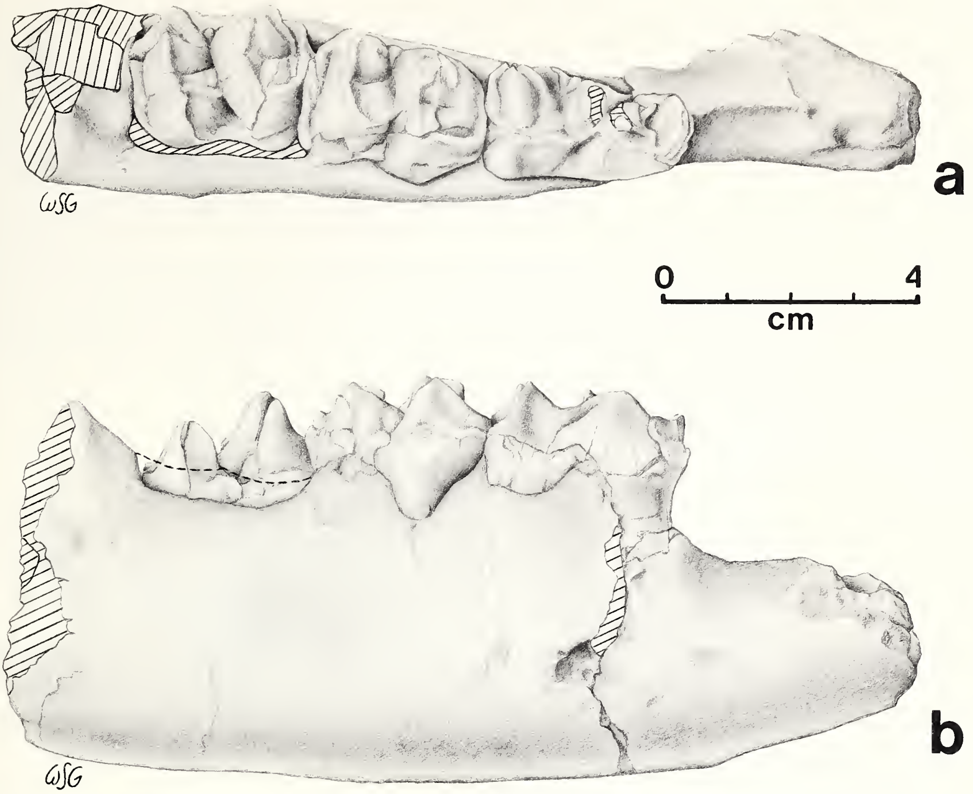

**Figure 6.** *Tapirus merriami,* occlusal view of right dentary F:AM 17840 with $DP_{2-4}$. Broken surfaces are represented by parallel lines.

UCMP V65099/28800, right $M^3$ (Stirton and Weddle, 1929); LACM 1066/1606, fragment of left upper cheek tooth; LACM 1754/4862, partial mandible with right $DP_4$, $P_2$–$M_3$ and left $DP_{2-4}$ and $P_2$–$M_3$; UCMP 570601/49022, right dentary with lower C, $DP_{2-4}$ and $M_1$; LACM 4629/121560, fragment of anterior left dentary with $P_2$ and posterior left dentary with $M_{2-3}$; LACM 5481/127688, posterior portion of right dentary with $M_{1-3}$ (Jefferson, 1986); UALP (cast from Borth private collection), posterior portion of right dentary with $DP_4$ and $M_{1-2}$; LACM 1068/1354, incomplete right dentary with lower I and $M_3$ (Miller, 1971); SDSNH 2321/20301, anterior portion of mandible with right $I_1$ and left $I_{2-3}$ and $P_{3-4}$ (Shaw, 1981; Lindsay, 1984); LACM 1066/31440, posterior portion of left dentary with $M_3$; LACM 1066/26698, right $M_1$; UCMP V65033/8747, left $M_2$ (or $M_1$?) (holotype of *T. californicus*) (Merriam, 1913; Stirton and Weddle, 1929; Simpson, 1945; Ray and Sanders, 1984); LACM(CIT) 594/3340, left $M_2$ (Stock, 1944); LACM 1066/1360, fragment of left lower cheek tooth; LACM 2031, tooth (Miller, 1971); LACM 1066/20549, anterior portion right dentary; LACM 1066/31441, fragment of dentary (Miller, 1971); LACMHC Pit 77/10524, left ectocuneiform (Harris and Jefferson, 1985); LACM 1066/20550, left third metacarpal; UCMP 3874/24249, first phalanx (Stock, 1930); UCMP 3874/24250, second phalanx (Stock, 1930).

**DISCUSSION.** Although *Tapirus californicus* Merriam, 1913, and *T. veroensis* Sellards, 1918, may be conspecific (see Summary of Systematics and Nominal Species), the small Pleistocene tapirs from the western USA are here referred to *T. californicus.*

**DESCRIPTION.** The type specimen of *Tapirus californicus* (UCMPV 65033/8747) from Woods Creek near Sonora, California, was tentatively identified as a left $M_2$ by Merriam (1913). Both Simpson (1945) and Ray and Sanders (1984) prefer Merriam's identification, but caution that the tooth may be a $P_4$. However, the size of the specimen (Table 4) closely approaches the mean size of the $M_1$ in the Florida sample of *T. veroensis* (Table 5) (Lundelius and Slaughter, 1976). Its length and anterior transverse dimensions overlap with only the smallest $M_2$ of *T. veroensis.* In UCMP 65033/8747, the anterior width is nearly equal to the posterior width. The relatively greater width of the posterior loph compared to the anterior loph in the $P_4$ (Table 5) precludes a firm assignment of this tooth as a $P_4$. UCMPV 65033/8747 is comparable in size and shape to other first molars in dentaries from Cali-

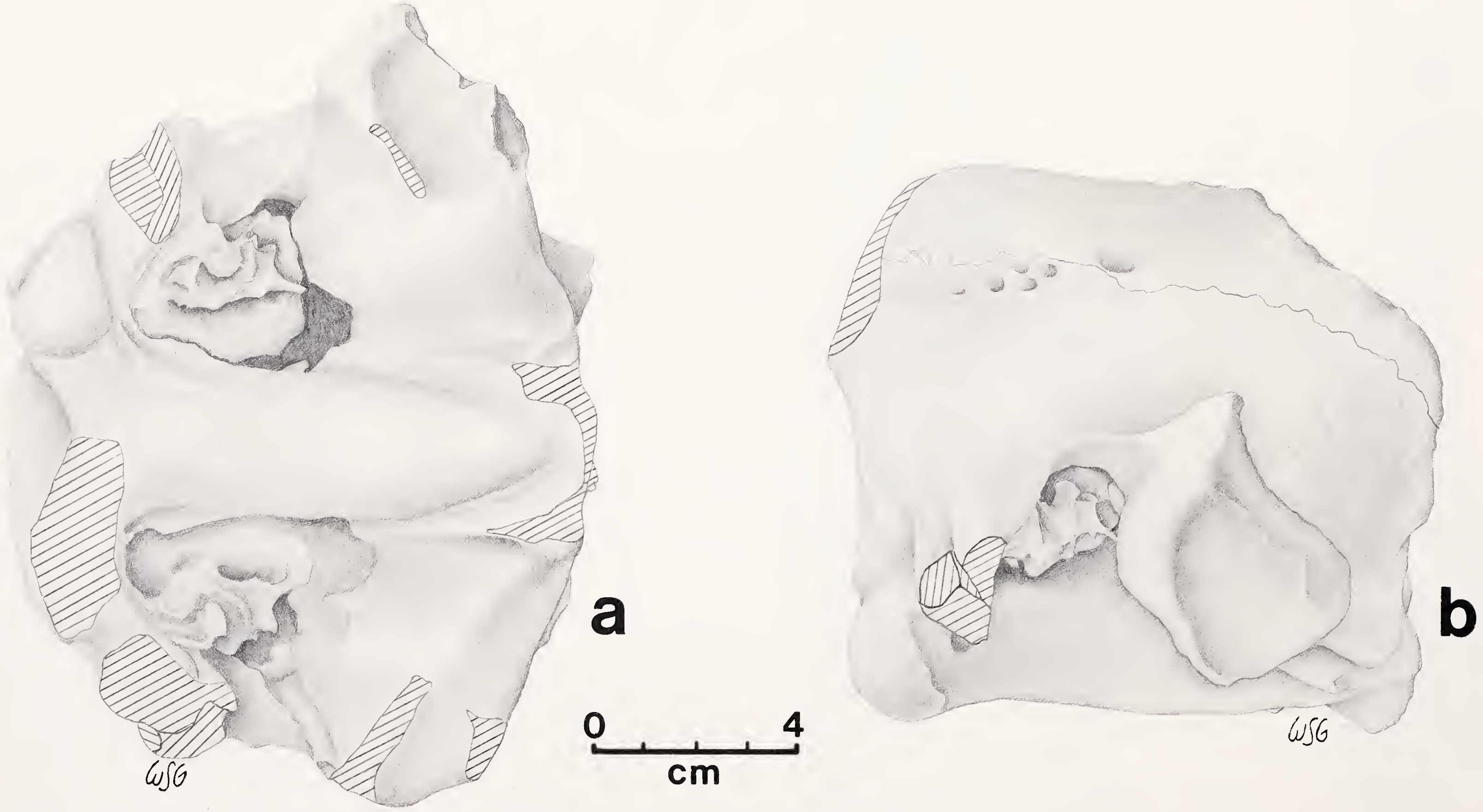

**Figure 7.** *Tapirus merriami*, ventral (a) and right lateral (b) views of skull LACM 6601/16057. Broken surfaces are represented by parallel lines.

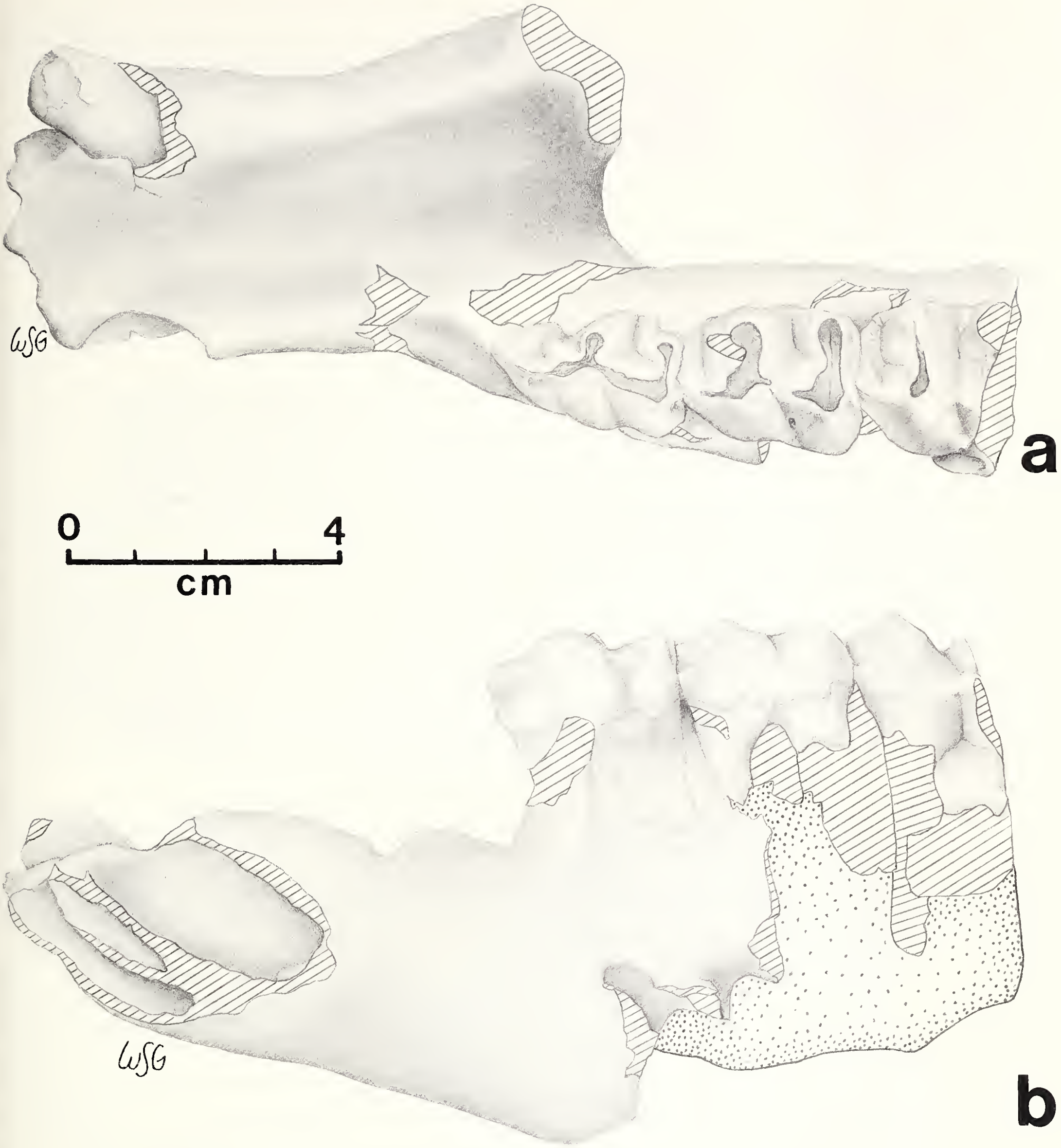

**Figure 8.** *Tapirus merriami,* occlusal (a) and left lateral (b) views of partial mandible LACM 6601/16057. Broken surfaces are represented by parallel lines. Sedimentary matrix is indicated by the stipple pattern.

fornia (Table 4), here referred to *T. californicus.* The type specimen of *T. californicus* should be considered an $M_1$. The presence of a small tubercle on the labial margin of the type specimen of *T. californicus* was used by Sellards (1918) to separate it from the paratype of *T. veroensis.* The expression of this character is variable in the inferior dentition of *T. californicus.*

The original maxilla and dentition of LACM 1087/125981 (cast) from Rolling Hills Estates, Los Angeles County, were housed in the collections of the Cabrillo Beach Museum, San Pedro, but could not be located. However, measurements from the high-quality cast (Table 6) fall well within the observed size range (Table 5) of *Tapirus veroensis* from Florida and Texas (Lundelius and Slaughter, 1976). The $P^4$ described by Stock (1944) and UCMP V71081/28800, a right $M^3$ (Stirton and Weddle, 1929), are also indistinguishable in size from *T. veroensis* (Tables 5 and 6).

The right $M^{1-3}$, CAS 101, was the only superior dentition of *Tapirus californicus* available to Sellards (1918) for comparison. He noted that this specimen lacked the incised line that is located posterior to the buttress or ridge that supports the lingual face of the paracone in the holotype of *T.*

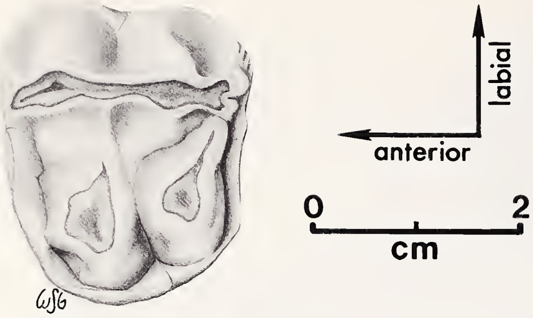

**Figure 9.** *Tapirus merriami,* occlusal view of right P$^2$ UCMPV 45005/38232.

*veroensis.* LACM 1087/125981 shares this condition with CAS 101. However, this feature on the P$^4$ described by Stock (1944) and on the M$^3$, UCMP V71081/28800, is similar to the type of *T. veroensis.* Sellards (1918) also used the external (labial) position of the parastyle to distinguish the holotype of *T. veroensis* from CAS 101. The parastyle is placed more labially in the Florida specimen than in CAS 101. Parastyle position in LACM 1087/125981 is similar to the holotype of *T. veroensis.*

The size of the partial lower left dentition, LACM 5481/127688 (Table 4; Fig. 11), from Rancho La Brea (Jefferson, 1986) falls within the upper half of the observed size range of *Tapirus veroensis* from Florida (Table 5). The specimen exhibits some abrasion and stream-transport damage. It represents a mature individual with the occlusal surface of M$_1$ fully worn and slightly cupped, M$_2$ in full wear, and M$_3$ coming into occlusion. Interdental wear between the M$_1$ and M$_2$ has removed approximately 1 mm of enamel and dentine from the posterior margin of the M$_1$. Similar wear between the M$_2$ and M$_3$ has worn approximately 1 mm from the anterior margin of the M$_3$.

F:AM 17844E, a right P$_1$ and F:AM 17844D, a left M$_1$, supposedly from El Casco, California, are distinctly smaller than the other tapir remains identified as *Tapirus merriami* in the collections from that site. The dimensions of these teeth fall within the size range of other specimens referred to *T. californicus* or *T. veroensis* (Tables 5 and 6). However, the locality data for F:AM 17844D and 17844E, recorded as "El Casco" and "? El Casco," respectively, are suspect (R.H. Tedford, pers. comm., 1987). Furthermore, the preservation of the specimens is unlike any other teeth from the site. The age of the El Casco fauna is estimated at 1.5 ± 0.3 myr (Reynolds and Reeder, 1986), about 1 myr older than any other small tapir remains from the western USA. If these specimens were collected from El Casco, which is doubtful, the temporal

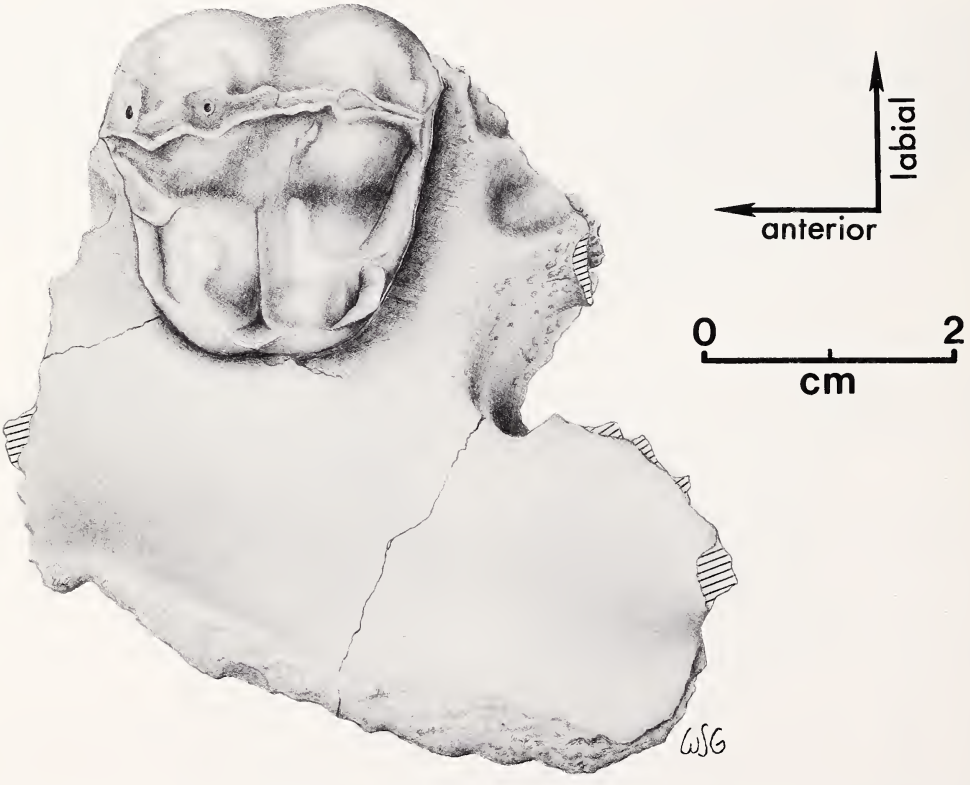

**Figure 10.** *Tapirus merriami,* occlusal view of left P$^2$ RCIC LC 47/361. Broken surfaces are represented by parallel lines.

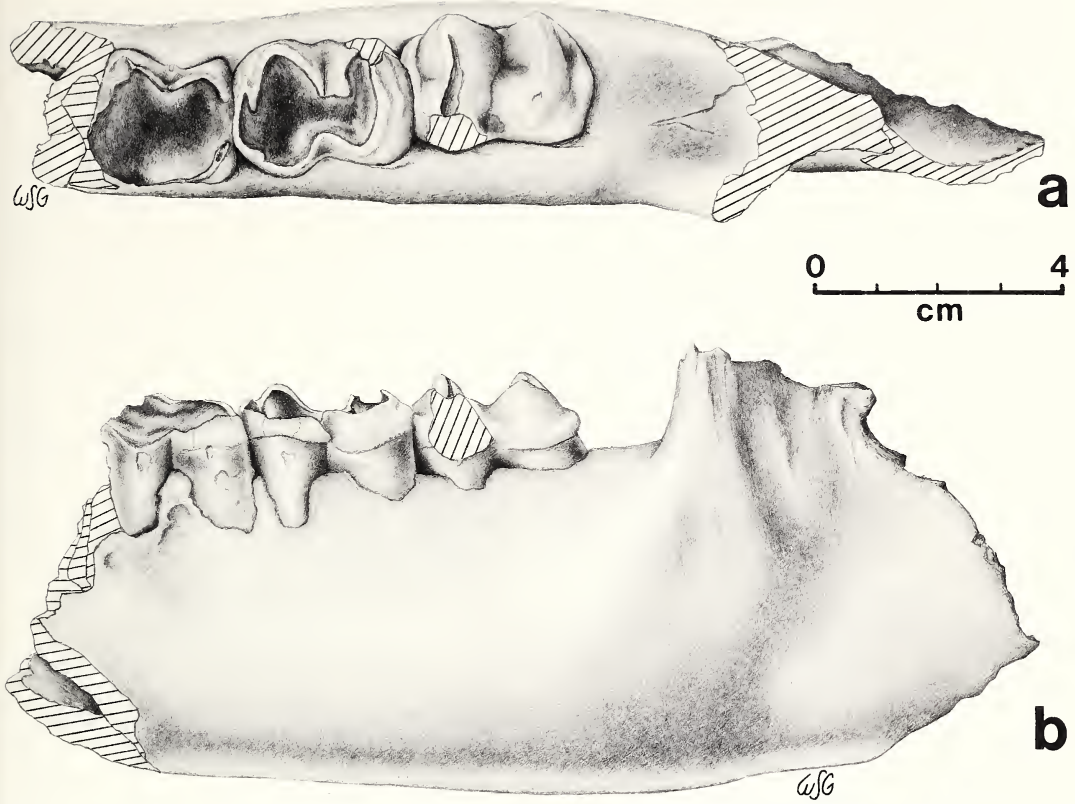

**Figure 11.** *Tapirus californicus,* occlusal view of right dentary LACM 5481/127688 with $M_{1-3}$. Broken surfaces are represented by parallel lines.

range of the taxon would be extended from late to early Irvingtonian.

Measurements of all other partial lower dentitions and isolated lower cheek teeth from California (Table 4) (Merriam, 1913; Stirton and Weddle, 1929; Stock, 1944; Miller, 1971), Oregon (Merriam, 1913; Leffler, 1964), and Sonora, Mexico (Shaw, 1981), fall within the observed size range of the Florida sample of *Tapirus veroensis* (Table 5).

Isolated, post-cranial specimens from Rancho La Brea (LACMHC Pit 77/10524, left ectocuneiform; UCMP 3874/24249, first phalanx; UCMP 3874/24250, second phalanx) and Newport Bay mesa (LACM 1066/20550, left third metacarpal) are tentatively referred to *Tapirus californicus* on the basis of their small size relative to *T. haysii* and *T. merriami.*

## *Tapirus* sp.

**REFERRED MATERIALS.** IVCM 570/2026, cranial fragments; ASM (no numbers), 21 isolated cheek tooth fragments (locality numbers not given; Colbert, 1950); $M^{1-2}$ (specimen and locality numbers not given; Leffler, 1964); LACM 2031, tooth (Miller, 1971); tooth (specimen and locality numbers not given; Mann, 1955); F:AM 17844F, 17844G, 17844H, and 17844J, upper cheek tooth fragments, and F:AM 17844I, lower cheek tooth fragment; IVCM 22/66, left innominate fragment; ASM (no number), questionable right second metatarsal (Colbert, 1950); LACM 1100/64039, distal portion of metacarpal or metatarsal.

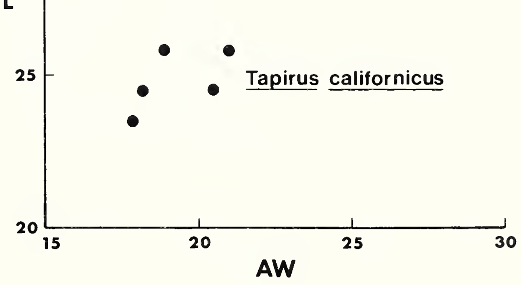

**Figure 12.** Bivariate distribution of the length (L) and anterior width (AW) (mm) of $M_2$ in *Tapirus merriami* and *T. californicus.* Measurements from Tables 1 and 4.

Table 4. Comparative measurements (mm) of lower cheek teeth of western North American specimens referred to *Tapirus californicus*. Explanation: * = measurement approximate/estimate; + = specimen damaged, minimum measurement

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| LACM 1354 | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | · | · | · | · | · | · | 28.7 | 19.6 | 16.8 |
| LACM 3340 | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | · | · | · | 28.0 | 19.2 | 16.8 | · | · | · |
| LACM 4862 | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 22.3 | 16.4 | 14.9 | 24.5* | 18.2 | 16.4 | · | · | · |
| LACM 26698 | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 25.1 | 17.1 | 15.6 | · | · | · | · | · | · |
| LACM 31440 | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | · | · | · | · | · | · | 27.5 | 19.3 | 16.9 |
| LACM 121506 | | $P_2$ | | | | | | | |
| | L | TW | — | | | | | | |
| | 23.6 | 15.6 | | | | | | | |
| | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | · | 16.9 | · | 25.7 | 18.9 | 18.0 | 26.4 | 19.9 | 18.3 |
| LACM 127688 | | $M_1$ | | | $M_2$ | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 22.2 | 20.8 | 19.7 | 27.5 | 21.0 | 19.8* | 29.1 | 21.3 | 19.2 |
| SDSNH 20301 | | $P_3$ | | | $P_4$ | | | | |
| | L | AW | PW | L | AW | PW | | | |
| | 25.4* | · | 15.6* | 23.0 | 17.8 | 18.5 | | | |
| UALP Borth | | $DP_4$ | | | $M_1$ | | | $M_2$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 24.5 | 16.0 | 17.5 | 24.9 | 18.3 | 17.6 | 24.5* | 20.5 | 19.0* |
| UCMPV 8747 | | $M_1$ | | | $M_2$ (1?) | | | $M_3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | · | · | · | 23.5 | 17.8 | 17.6* | · | · | · |
| UCMPV 49022 | | $DP_2$ | | | $DP_3$ | | | $DP_4$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 24.2 | · | 13.6 | 20.5 | 13.2 | 14+ | 22.0 | 14.5 | 14.2 |
| | | $M_1$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 22.4 | 16.2 | 15.7 | | | | | | |

**DESCRIPTION.** The uncatalogued fragmentary remains from Ventana Cave, Arizona, reported by Colbert (1950) fall within the temporal and geographic range of *Tapirus merriami*. The three cheek tooth fragments (field numbers VIII-P-189-X and IX-P-189-X) figured by Colbert (1950) appear to represent a large form, but provide no comparative measurements and are specifically nondiagnostic.

Leffler (1964) described, but did not present dental measurements for, a partial maxilla with $M^{1-2}$ collected from the Blancan, lower member of the San Diego Formation in San Diego. The specimen could not be located in the LACM, SDSNH, or UCMP collections (T.A. Deméré, pers. comm., 1986).

The cranial specimen, IVCM 570/2026, from Blancan deposits in the Anza-Borrego Desert is very incomplete and includes a fragment of the premaxilla/maxilla, supraorbital portion of the parietal and a partial jugal. The vertical depth of the jugal taken at a point immediately lateral to the supraorbital process measures 46.7 mm. IVCM 22/66, a partial acetabulum and fragment of pubis, is very incomplete and only tentatively referred to *Tapirus* sp.

The Irvingtonian specimen mentioned by Mann (1955) from Murrieta, California, could not be located. A tooth referred to *Tapirus* sp. by Miller (1971) from Long Beach, California, was not located in the LACM collection. Although relatively large, the incomplete metapodial, LACM 1100/64039, from Rancholabrean deposits in Orange County, California, is specifically indeterminate.

## CONCLUSIONS

### LARGE TAPIRS

The large, late Pliocene and Pleistocene specimens from the Pacific coast either exceed or fall within the upper portion of the size range of *Tapirus haysii* from the eastern USA. Measurements of the Blancan, Porter Ranch specimen, the early Irvingtonian type of *T. merriami* from Bautista Creek (Frick, 1921), and the early Irvingtonian El Casco, California, specimens exceed the observed size range of some or all dental parameters of the sample of *T. haysii* from Port Kennedy, Pennsylvania (Simpson, 1945), and are comparable to or larger than the topotypic sample of *T. haysii* from the Neuse River, North Carolina (Ray and Sanders, 1984). The pre-Rancholabrean maxillae from Alameda County, California, are also large in comparison to the eastern USA samples. Lower dentitions from the lower Rancholabrean of Arizona exceed the observed size range of *T. haysii,* and for some dental measurements, exceed the size of the type of *T. merriami.*

The size of the measurable permanent teeth in the late Blancan juvenile skull and partial mandible from Tapiado Wash, California, is within (or exceeds) the size range exhibited by the Port Kennedy sample of *Tapirus haysii.* Furthermore the $P^2$ in this specimen, the Irvingtonian specimen from the Chicago Clay Pit in Alameda County, and the Rancholabrean $P^2$ from R. Clark Regional Park, Orange County, California, do not exhibit the advanced degree of molarization that typifies the Port Kennedy tapir (Simpson, 1945).

These characters (consistently large size and the lack of a well developed protoloph on the $P^2$) support the recognition of a specifically distinct population of *Tapirus* in the upper Blancan through upper Rancholabrean record from the western USA.

**Table 5. Comparative measurements (mm) and observed size range of cheek teeth of *Tapirus veroensis* from the central and eastern United States (measurements from Lundelius and Slaughter, 1976).**

***Tapirus veroensis***
**Rancholabrean of Florida**

| | L | AW | PW |
|---|---|---|---|
| $P^1$ | 17.5–20.8 | TW 14.9–18.6 | — |
| $P^2$ | 18.7–21.1 | 19.6–23.2 | 22.8–25.8 |
| $P^3$ | 19.0–22.0 | 22.0–26.3 | 24.1–26.5 |
| $P^4$ | 20.0–22.9 | 24.2–28.6 | 22.5–28.8 |
| $M^1$ | 20.2–23.8 | 24.2–28.4 | 22.3–26.2 |
| $M^2$ | 23.5–27.0 | 26.3–31.1 | 23.8–28.4 |
| $M^3$ | 23.5–26.1 | 28.0–32.1 | 23.1–28.1 |
| $P_2$ | 22.3–28.5 | TW 13.8–19.1 | — |
| $P_3$ | 20.0–24.5 | 15.1–17.5 | 16.0–21.4 |
| $P_4$ | 20.2–25.2 | 15.9–20.6 | 15.9–22.0 |
| $M_1$ | 20.0–26.9 | 17.0–22.0 | 17.5–22.8 |
| $M_2$ | 22.5–29.0 | 18.4–23.4 | 17.8–22.8 |
| $M_3$ | 25.4–32.2 | 19.0–23.1 | 17.0–21.7 |

***Tapirus veroensis***
**Rancholabrean of Texas**

| | L | AW | PW |
|---|---|---|---|
| $P^1$ | 19.2–20.4 | TW 14.5–19.6 | — |
| $P^2$ | 19.8–20.5 | 21.1–23.9 | 22.4–25.9 |
| $P^3$ | 20.6–23.5 | 25.8–27.6 | 25.0–27.6 |
| $M^1$ | 22.6–25.6 | 25.2–29.2 | 24.0–27.2 |
| $M^2$ | 25.7–27.4 | 30.3–31.1 | 26.5–29.0 |
| $M^3$ | 23.7–28.5 | 27.6–32.9 | 22.3–29.1 |

This population must be assigned to *T. merriami* Frick, 1921.

### SMALL TAPIRS

The records of a small, western USA tapir extend from upper Irvingtonian through the upper Rancholabrean. This form is here referred to *Tapirus californicus.* No consistently distinctive morphological dental parameters have been found to successfully distinguish *T. californicus* from *T. veroensis* (Ray and Sanders, 1984). Although *T. californicus* takes precedence over *T. veroensis,* no authors have attempted to revise the taxonomic status of these two species, mainly because *T. veroensis* is morphologically well defined and the name has been widely applied. Any revisions must wait until more definitive cranial materials assignable to *T. californicus* are recovered.

### SUMMARY

Regardless of which names are applied, a pattern in the temporal and geographic distribution of western USA tapirs is apparent. A large species, here referred to Frick's *Tapirus merriami,* typically occurs in upper Pliocene (upper Blancan) and lower

**Table 6.** Comparative measurements (mm) of upper cheek teeth of western North American specimens referred to *Tapirus californicus*. Explanation: * = measurement approximate/estimate; + = specimen damaged, minimum measurement.

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| CAS 101 | | $M^1$ | | | $M^2$ | | | $M^3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 21.9 | 27.5 | 24.9 | 25.4 | 30.8 | 26.8 | 26.3 | 29.5 | 24.1 |
| F:AM 17844E | | $P^1$ | | | | | | | |
| | L | TW | — | | | | | | |
| | 19.8 | 19.4 | | | | | | | |
| F:AM 17846D | | $M^1$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 22.9 | 28.3 | 27.3 | | | | | | |
| LACM 125981 | | $P^2$ | | | $P^3$ | | | $P^4$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 20.5+ | 24* | · | 22.7+ | 27* | · | 22.5+ | 29.6 | 28.7 |
| | | $M^1$ | | | $M^2$ | | | $M^3$ | |
| | L | AW | PW | L | AW | PW | L | AW | PW |
| | 23.6 | 28.9 | · | 27.2 | 31.8 | · | · | 29.9 | · |
| UCMPV 28800 | | $M^3$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 26* | 24* | 20* | | | | | | |
| (Stock, 1944) | | $P^4$ | | | | | | | |
| | L | AW | PW | | | | | | |
| | 21.1 | 28* | 27.9* | | | | | | |

to middle Pleistocene (Irvingtonian) deposits along the Pacific coast. It is poorly known from upper Pleistocene (Rancholabrean) deposits in California, but is found in the Rancholabrean of Arizona.

A small species, poorly represented in the late Irvingtonian, is typically found in coastal California deposits of Rancholabrean age. This small taxon, *Tapirus californicus,* has not been found in more inland, western USA assemblages from California, Arizona, or Nevada. Although the temporal range of large and small tapirs overlaps during late Irvingtonian through late Rancholabrean time, they are found together only in the Rancholabrean Palos Verdes Sand of coastal Orange County, California.

## ACKNOWLEDGMENTS

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of Los Angeles County
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# CONTRIBUTIONS IN SCIENCE

## NEW SLIT-LIMPETS (SCISSURELLACEA AND FISSURELLACEA) FROM HYDROTHERMAL VENTS. PART 1. SYSTEMATIC DESCRIPTIONS AND COMPARISONS BASED ON SHELL AND RADULAR CHARACTERS

JAMES H. MCLEAN

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of Los Angeles County
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# NEW SLIT-LIMPETS (SCISSURELLACEA AND FISSURELLACEA) FROM HYDROTHERMAL VENTS. PART 1. SYSTEMATIC DESCRIPTIONS AND COMPARISONS BASED ON SHELL AND RADULAR CHARACTERS

JAMES H. MCLEAN[1]

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[1] Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007.

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**ABSTRACT.** Six new species of slit-limpets endemic to the deep-sea hydrothermal-vent habitat have similar shells and similar external anatomy, but are placed in two families in separate superfamilies: Scissurellacea and Fissurellacea.

Taxonomic innovations for Scissurellacea (raised from family level by Haszprunar [1989]) include the recognition of four subfamilies in Scissurellidae: new subfamily Temnocinclinae with two new genera having open slits: *Temnocinclis,* monotypic for *T. euripes* new species from the Juan de Fuca Ridge, and *Temnozaga,* monotypic for *T. parilis* from 21°N on the East Pacific Rise; new subfamily Sutilizoninae: *Sutilizona* new genus with a closed slit, monotypic for *S. theca* from 12°N on the East Pacific Rise. Non-hydrothermal-vent scissurellids are retained in the new subfamily Anatominae and the typical subfamily Scissurellinae. Subfamilies are defined on the basis of shared protoconch, radular, and gill characters.

Taxonomic innovations for Fissurellacea are the new family Clypeosectidae with two new genera: *Clypeosectus* with an open slit, and *Pseudorimula* with a closed slit and a unique, tripartite shell muscle. *Clypeosectus* has two new species, type species *C. delectus* from the Galapagos Rift and the East Pacific Rise at 13°N and 21°N, and *C. curvus* from the Juan de Fuca Ridge and the Explorer Ridge. *Pseudorimula* is monotypic for *P. marianae* new species from the Mariana Back-Arc Basin vents.

Study of anatomy by Haszprunar (1989) confirms the need for the new higher taxa, which are based on anatomical characters as well as shell and radular characters. As in all other scissurellids, there are no reproductive specializations in the new vent-associated scissurellid limpets. Clypeosectids have such fissurellacean characters as a reduced left kidney and anal gland, but differ in having a unique radula and a pedal gland, and lacking muscle hooks and pits on the early teleoconch; they further differ in being specialized for internal fertilization.

The new genera of both superfamilies lack the enlarged outermost lateral teeth that characterize the non-vent associated genera. This is interpreted as a convergent loss possibly due to a more easily processed food source of bacterial films in the hydrothermal-vent habitat.

As previously hypothesized for other hydrothermal-vent limpets, these groups may have entered the hydrothermal-vent habitat in the early Mesozoic, at the same time their superfamilies appeared and diversified in shallow water.

## INTRODUCTION

The recently discovered hydrothermal-vent community has produced a number of unusual new mollusks, among which gastropods of limpet form are exceptionally well represented. At latest summary (McLean, 1988b), seven superfamilies (four endemic) and eight families (seven endemic) were represented by 27 species.

Radulae characteristic of some of the hydrothermal-vent limpet groups have been illustrated (Hickman, 1983) prior to their formal descriptions. Except for the slit-limpets, brief preliminary notes on external features of the new groups of hydrothermal-vent limpets have been given by McLean (1985). Protoconchs and immature shells of many of the limpets, including two species of slit-limpets, have also been illustrated (Turner et al., 1985), although not identified to family or species.

To date, five new families of limpets from hydrothermal vents have been described: Neomphalidae in the new superfamily Neomphalacea (McLean, 1981), anatomy by Fretter et al. (1981); Pyropeltidae in the existing superfamily Lepetellacea (McLean and Haszprunar, 1987); Lepetodrilidae and Gorgoleptidae in the new superfamily Lepetodrilacea (McLean, 1988a), anatomy by Fretter (1988); and Peltospiridae in the new superfamily Peltospiracea (McLean, 1989), anatomy by Fretter (1989).

Slit-limpets from the hydrothermal-vent community were first noted by Turner (1980), who illustrated a shell of the species from the Galapagos Rift that is here described as *Clypeosectus delectus.* Other illustrations of shells of slit-limpets from the Galapagos Rift and from the East Pacific Rise at 21°N have been given by Lutz et al. (1984), Turner and Lutz (1984), and Turner et al. (1985), who also included a species from 21°N identified as an "unnamed *Rimula*(?)," which is here described as *Temnozaga parilis.*

The caption to Turner's (1980) first figure of a slit-limpet (the species here described as *Clypeosectus delectus*) stated that "it is probably a living representative of a genus known in the fossil record from the Upper Jurassic to the Eocene." That allocation surely alluded to *Loxotoma* Fischer, 1885, a fissurellid that had a markedly asymmetrical slit (see Knight et al., 1960, fig. 141-7). On shell characters, however, the slit-limpets lack the pits that characterize the early teleoconch sculpture of all fissurellids (e.g., see Bandel, 1982, pl. 11, fig. 11). Hickman (1983) figured the radula of the same species from the Galapagos Rift, noting that it is unlike that of fissurellids, and concluded that the species is but "questionably allied to the Fissurellidae."

Although shells of the six species described here may suggest (except for the lack of pits) that these are fissurellid limpets, the first impression derived from the external morphology suggests that all are scissurellids, because all have a large anterior pedal gland (which is lacking in fissurellids) and all have relatively few epipodial tentacles (as in scissurellids, not fissurellids). In view of the unique radula previously figured by Hickman (1983), a study of the internal anatomy was necessary to establish relationships. Anatomy of these species is treated by Haszprunar (1989) in Part 2. His investigation of anatomy has indicated that a new family related to Fissurellidae should be erected for three species in two genera having the bizarre radular type originally figured by Hickman, and that limpets of the family Scissurellidae are also present in the hydrothermal-vent community. The new scissurellids, however, have modified scissurellid radulae.

## MATERIALS AND METHODS

Slit-limpets were found when the deep-sea hydrothermal-vent biological community was discovered in 1979 along the Galapagos Rift by the Woods Hole submersible *Alvin* (Corliss et al., 1979; Hessler and Smithey, 1983). In 1979, slit-limpets were again collected by the *Alvin* at the Galapagos Rift and at the East Pacific Rise at 21°N (Spiess et al., 1980; Hessler et al., 1985). In 1982, the limpets were collected at 13°N on the East Pacific Rise by a French expedition using the submersible *Cyana* (Desbruyeres et al., 1982; Desbruyeres and Laubier, 1983). Two additional species described here were first collected in 1983 with the submersible *Pisces IV* on the Juan de Fuca Ridge by a Canadian expedition (Chase et al., 1985; Tunnicliffe et al., 1985). Jones et al. (1985) give station data for all dives made by these submersibles through 1985.

Yet another species was discovered with the *Alvin* in 1987 at the Mariana Back-Arc Basin vents in the western Pacific (Hessler et al., 1988). The most recently discovered species was collected with the *Alvin* in March, 1988, on the East Pacific Rise at 12°N.

Hydrothermal-vent sites investigated by the *Alvin* that have not yielded slit-limpets are the Guaymas Basin, first visited in 1982, and the Florida Escarpment, first visited in 1984.

Mollusks were collected as part of the sampling program on most dives made by submersibles at hydrothermal-vent sites (for details of collecting procedures see Turner et al., 1985). Many of the limpets were collected along with samples of vestimentiferan tube worms by the mechanical arms of the submersibles. Specimens were dead on reaching the surface and were originally fixed for 24 hours in 5% seawater formalin buffered with sodium borate, washed in freshwater, and transferred to 70% ethanol.

Unlike all other newly described limpet groups from hydrothermal vents, none of the slit-limpets was abundant. For most species the number available was barely sufficient for description and, in some cases, not enough to provide specimens of both sexes for sectioning. Station data and numbers of specimens for dives yielding slit-limpets are summarized in Table 1. Measurements and disposition of all examined specimens are given in Table 2.

Except for Figures 4B,C and 9A–F, which have previously been published by Turner et al. (1985), and Figure 11A, previously published by Hickman (1983), the illustrations in this paper result from photographic and SEM work at the Natural History Museum of Los Angeles County.

Type material is placed in the Natural History Museum of Los Angeles County (LACM), the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), the Museum National d'Histoire Naturelle, Paris (NMNH), and the National Museum of Natural History, Washington, D.C. (USNM).

## SYSTEMATICS

## Order ARCHAEOGASTROPODA
Thiele, 1925

## Suborder VETIGASTROPODA
Salvini-Plawen, 1980

Recent authors (Salvini-Plawen, 1980; Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988a, 1988b; Hickman, 1988) have discussed the problems inherent in the archaeogastropod concept, pointing out that the order Archaeogastropoda, as traditionally constituted (Thiele, 1925; Knight et al., 1960), represents a grade. Although Hickman (1988) has redefined and limited Archaeogastropoda to cover those superfamilies now treated by Salvini-Plawen and Haszprunar (1987) as the suborder Vetigastropoda (in so doing making Vetigastropoda a synonym of Archaeogastropoda), I have elected to follow Haszprunar (1988a, 1988b) in a classification scheme that allows Archaeogastropoda as an "orthophyletic grade" and Vetigastropoda as a clade.

## Superfamily SCISSURELLACEA
Gray, 1847

Justification for the removal of Scissurellidae from the Pleurotomariacea and elevation to superfamilial status is given by Haszprunar in (1989). As the superfamily contains but a single living family, the diagnosis that follows serves for that of the superfamily and family.

## Family SCISSURELLIDAE
Gray, 1847

**DESCRIPTION.** Coiled or limpetlike, interior nacre lacking, with shell slit, two shell muscles, and operculum. Protoconch finely reticulate (sometimes finely pitted), or with strong collabral ridges. Eyes (if present) with closed vesicles. Operculum retained in all genera. Rachidian tooth broad, base of shaft with lateral projections; overhanging cusp broad with one main denticle and smaller lateral denticles; lateral teeth narrow, cusps with several sharp denticles, shafts with laterally directed elbow; enlarged outer lateral present or absent; marginal teeth numerous.

**REMARKS.** Herbert (1986) has reviewed the systematics of Scissurellidae and discussed the shell and protoconch characters upon which the relatively few genera in the family have been based. Two groups were apparent, based on protoconch sculpture. The genera *Anatoma* Woodward, 1859, and *Sukashitrochus* Habe and Kosuge, 1964, have a finely reticulate protoconch, whereas the genera *Scissurella* d'Orbigny, 1824, and *Sinezona* Finlay, 1927, have strong collabral sculpture on the protoconch (Fig. 6C; see also Batten, 1975; Yaron, 1980; Bandel, 1982; Herbert, 1986). Here I add *Incisura* Hedley, 1904, to those with strong collabral sculpture (Fig. 6E). All of these genera have a basic radular plan in common: a broad, multicuspid rachidian tooth, three lateral teeth of similar morphology, and an enlarged outer lateral tooth with numerous cusps (Figs. 6F,G).

The three new scissurellid genera from the hydrothermal-vent habitat (*Temnocinclis*, *Temnozaga*, and *Sutilizona*) do not have the collabral sculpture on the protoconch and share certain features

Table 1. Station data and number of specimens from dives yielding slit-limpets.

| Dive | Depth (m) | Position | Date | Number |
|---|---|---|---|---|
| | | *Temnocinclis euripes* | | |
| | | *Alvin* dives, Endeavour Segment, Juan de Fuca Ridge | | |
| 1447 | 2213 | 47°57.0′N, 129°06.0′W | 03 Sep 1984 | 2 |
| 1452 | 2208 | 47°57.0′N, 129°0.60′W | 07 Sep 1984 | 2 |
| | | *Pisces IV* dive, Axial Seamount, Mid-Juan de Fuca Ridge | | |
| 1726 | 1575 | 45°59.5′N, 130°03.5′W | 27 Jul 1986 | 4 |
| | | *Alvin* dive, Southern Juan de Fuca Ridge | | |
| 1463 | 2250 | 44°39.2′N, 130°22.0′W | 24 Oct 1984 | 3 |
| | | *Temnozaga parilis* | | |
| | | *Alvin* dives, East Pacific Rise at 21°N | | |
| 1226 | 2616 | 20°50.0′N, 109°06.0′W | 10 May 1982 | 1 |
| 1229 | 2615 | 20°50.0′N, 109°06.0′W | 14 May 1982 | 1 |
| | | *Sutilizona theca* | | |
| | | *Alvin* dive, East Pacific Rise at 12°N | | |
| 2003 | 2715 | 11°46.0′N, 103°47.0′W | 25 Mar 1988 | 3 |
| | | *Clypeosectus delectus* | | |
| | | *Alvin* dives, Galapagos Rift | | |
| 733 | 2496 | 00°47.3′N, 86°07.8′W | 16 Mar 1977 | 1 |
| 880 | 2493 | 00°47.6′N, 86°06.4′W | 21 Jan 1979 | 1 + 1 juv. |
| 884 | 2482 | 00°48.1′N, 86°07.0′W | 25 Jan 1979 | 8 juv. |
| 890 | 2447 | 00°48.9′N, 86°13.3′W | 15 Feb 1979 | 1 |
| 895 | 2482 | 00°47.9′N, 86°09.3′W | 20 Feb 1979 | 2 + 1 juv. |
| 896 | 2460 | 00°48.2′N, 86°13.6′W | 21 Feb 1979 | 3 juv. |
| 984 | 2451 | 00°48.0′N, 86°13.0′W | 01 Dec 1979 | 3 |
| 989 | 2482 | 00°48.0′N, 86°09.0′W | 06 Dec 1979 | 1 |
| 991 | 2490 | 00°48.0′N, 86°09.0′W | 08 Dec 1979 | 1 |
| | | *Cyana* dive, East Pacific Rise at 13°N | | |
| 82-36 | 2633 | 12°48.6′N, 103°56.7′W | 13 Mar 1982 | 4 |
| | | *Alvin* dives, East Pacific Rise at 21°N | | |
| 1221 | 2618 | 20°50.0′N, 109°06.0′W | 04 May 1982 | 2 |
| 1222 | 2614 | 20°50.0′N, 109°06.0′W | 06 May 1982 | 1 |
| 1223 | 2616 | 20°50.0′N, 109°06.0′W | 07 May 1982 | 1 |
| 1226 | 2616 | 20°50.0′N, 109°06.0′W | 10 May 1982 | 10 + 8 juv. |
| | | *Clypeosectus curvus* | | |
| | | *Pisces IV* dive, Explorer Ridge | | |
| 1494 | 1818 | 49°45.6′N, 130°16.1′W | 01 Jul 1984 | 1 |
| | | *Alvin* dive, Endeavour Segment, Juan de Fuca Ridge | | |
| 1447 | 2213 | 47°57.0′N, 129°06.0′W | 03 Sep 1984 | 1 |
| | | *Pisces IV* dives, Axial Seamount, Mid-Juan de Fuca Ridge | | |
| 1729 | 1575 | 45°59.5′N, 130°03.5′W | 30 Jul 1986 | 1 |
| 1730 | 1575 | 45°59.5′N, 130°03.5′W | 31 Jul 1986 | 5 |
| 1733 | 1575 | 45°59.5′N, 130°03.5′W | 03 Aug 1986 | 2 |
| | | *Pseudorimula marianae* | | |
| | | *Alvin* dives, Mariana Back-Arc Basin | | |
| 1836 | 3660 | 18°10.95′N, 144°43.2′E | 27 Apr 1987 | 4 |
| 1843 | 3640 | 18°12.6′N, 144°42.4′E | 04 May 1987 | 1 |

of the external anatomy (monopectinate ctenidia, loss of eyes, cephalic tentacles lacking micropapillae). Additionally, they have a radular distinction in common: all lack the enlarged fourth lateral tooth. However, *Sutilizona* stands apart from *Temnocinclis* and *Temnozaga* in radular and protoconch characters. Because a number of shared characters can now be limited to groups of genera in Scissurellidae, it is necessary to recognize four groups at the subfamily level:

1. Anatominae, new subfamily for *Anatoma* and *Sukasitrochus.* Shell coiled, protoconch finely reticulate, radula with enlarged fourth lateral tooth, ctenidia bipectinate.
2. Scissurellinae, typical subfamily for *Scissurella, Sinezona,* and *Incisura.* Shell coiled or of limpet form, protoconch with strong axial ribs, radula with enlarged fourth lateral tooth, ctenidia bipectinate.
3. Temnocinclinae, new subfamily for the new genera *Temnocinclis* and *Temnozaga.* Shell of limpet form, protoconch finely reticulate, radula lacking enlarged fourth lateral tooth, ctenidia monopectinate.
4. Sutilizoninae, new subfamily for new genus *Sutilizona.* Shell of markedly asymmetrical limpet form, protoconch reticulate with deep pits, radula lacking enlarged fourth lateral tooth, marginal teeth similar to lateral teeth, ctenidia monopectinate.

The two new subfamilies (Temnocinclinae and Sutilizoninae) restricted to the hydrothermal-vent community are treated below in greater detail.

Waren and Bouchet (1989) illustrated a fragmentary specimen from *Alvin* dive 1214, East Pacific Rise near 21°N, identified as *Sinezona* sp., representing a scissurellid genus from shallow water. That record needs further confirmation before a species of *Sinezona* can be admitted to the hydrothermal-vent fauna.

## TEMNOCINCLINAE new subfamily

**TYPE GENUS.** *Temnocinclis* new genus.

**DESCRIPTION.** Shell of limpet form, nearly symmetrical; slit remaining open at maturity, slit-borders with interlocking projections; protoconch finely reticulate, lacking collabral ridges. Radula lacking enlarged fourth lateral tooth. Ctenidia monopectinate, of equal size and position; cephalic tentacles non-papillate, eyes lacking.

For anatomical characters see Haszprunar (1989).

**REMARKS.** Two new genera (*Temnocinclis* and *Temnozaga*) known only from the hydrothermal-vent habitat share the above characters. Both genera are monotypic. The two species are unusually large-sized members of the family. Unique characters of this subfamily are the finely reticulate protoconch and the interlocking edges of the slit-borders, particularly near the anterior tip. The monopectinate ctenidia, the lack of eyes, and the lack of sensory papillae on the cephalic and epipodial tentacles are shared with the new subfamily Sutilizoninae.

Investigation by Haszprunar (1989) shows that the internal anatomy of Temnocinclinae closely corresponds to that of shallow-water Scissurellidae, with no reproductive specializations, making this and the Sutilizoninae the only groups of hydrothermal-vent limpets not requiring the erection of a new family.

The limpet form in Scissurellidae is also known in *Incisura lytteltonensis* (E.A. Smith, 1894) (Figs. 6B,E,G), a species common in the intertidal zone in New Zealand. *Incisura* has a maximum length of 1.3 mm, which is about one-third the length of *Temnocinclis* and *Temnozaga. Incisura* continues to be erroneously assigned to Fissurellidae (e.g., by Powell, 1979:37, who had missed Bourne's (1910) study of the anatomy and radula). *Incisura* has an axially ridged protoconch (Fig. 6E) like that of *Sinezona* (Fig. 6C) and *Scissurella.* It lacks the sculptural elements of the teleoconch of other scissurellids and the slit-borders are not raised; it has an extremely short slit and selenizone (Fig. 6B). However, as in *Temnocinclis,* there is a reduction in the epipodial tentacles, compared to those of other scissurellids.

The extremely long slits of both *Temnocinclis* and *Temnozaga* are very different from the short slit of *Incisura* and appear to represent structural liabilities in the shell; yet, some stability and rigidity may result from the interlocking projections along the slit-borders (Figs. 1G, 2B).

The radula of temnocincline genera (Figs. 5A–D) agrees with that of other scissurellid genera in having little asymmetry between the left and right sides of the radular ribbon. Temnocincline genera lack the enlarged outer lateral tooth of other scissurellid genera, but the morphology of the rachidian and inner lateral teeth is clearly comparable to the condition in other scissurellid genera.

### KEY TO GENERA

Apical whorl overhanging posterior end of shell . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Temnocinclis*
Apical whorl not overhanging shell posterior . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Temnozaga*

## *Temnocinclis* new genus

**TYPE SPECIES.** *Temnocinclis euripes* new species.

**DESCRIPTION.** Shell elongate, relatively high; apical whorl posterior to apertural margin, not raised above it. Protoconch sculpture unknown (all specimens heavily coated with mineral deposits). Sculpture sharply clathrate; slit-borders raised, with interlocking projections in contact at anterior end. Broad band of periostracum stretched posteriorly across excavated columellar region of shell.

**External Anatomy.** Cephalic tentacles and ctenidia as diagnosed for subfamily. Three posterior pairs of epipodial tentacles; operculum small, multispiral, early volutions with raised edges.

**Radula.** Rachidian tooth broad, multicuspid; lat-

**Table 2.** Dive numbers, figure numbers, museum catalog numbers of holotypes and paratypes, dimensions, and condition of slit-limpet specimens. Except where indicated as dry, most specimens are maintained in alcohol because shells are decalcified at the margins. Dimensions are given in the order: length, width, and height.

| Dive | Figure | Museum no. | Dimensions (mm) | Condition |
|---|---|---|---|---|
| *Temnocinclis euripes* | | | | |
| 1447a | — | USNM 859962 | 2.9 × 2.0 × 1.6 | Shell decalcified at margin, body intact |
| 1447b | 1E,F | LACM 2351 | — — — | Shell fragmented, body sectioned (female) |
| 1452 | 5A,B | USNM 859963 | 3.7 × 2.3 × 1.6 | Shell decalcified at margin, radula used |
| 1726a | 1A–C | USNM 859964 | 3.8 × 2.4 × 1.5 | Holotype, shell dry, body sectioned (male) |
| 1726b | 1G,H | LACM 2352a | 4.0 × 2.7 × 1.8 | Shell decalcified at margin, body intact |
| 1726c | 4A | LACM 2352b | 2.5 × 1.6 × — | Shell dry, scanned, body intact |
| 1726d | — | USNM 859965 | 1.8 × 1.3 × 0.7 | Shell decalcified at margin, body intact |
| 1463a | 1D | LACM 2353a | 3.8 × 2.4 × 1.7 | Shell decalcified at margin, body intact |
| 1463b | — | LACM 2353b | — — — | Shell crushed, body intact |
| 1463c | — | MCZ 297060 | 3.8 × 2.5 × 1.7 | Shell decalcified at margin, body intact |
| *Temnozaga parilis* | | | | |
| 1226 | 2A–F, 4B,C | USNM 859966 | 4.1 × 3.0 × 1.7 | Holotype, Turner et al., 1985, fig. 11 |
| 1229 | 2G,H, 5C,D | LACM 2354 | — — — | Shell missing, radula used, operculum intact |
| *Sutilizona theca* | | | | |
| 2003a | 4D–F,3C | USNM 859967 | 1.3 × 0.9 × 0.5 | Holotype, shell scanned, body sectioned |
| 2003b | 3A,B | LACM 2355a | 1.3 × 0.9 × 0.5 | Shell broken, body sectioned |
| 2003c | E,F | LACM 2355b | — — — | Shell in fragments, radula used |
| *Clypeosectus delectus* | | | | |
| — | 9A–C | — — | 1.9 × 1.4 — | Turner et al., 1985, fig. 9 |
| 733 | 11A | — — | — — — | Hickman, 1983, fig. 5, radula |
| 880a | — | LACM 2356a | — — — | Shell broken (ca. 3 mm), no body |
| 880b | — | LACM 2356b | — — — | 1 decalcified juvenile under 1 mm |
| 884 | — | USNM 859968 | — — — | 8 decalcified juveniles under 1 mm |
| 890 | — | USNM 859969 | 1.8 × 1.3 × 0.4 | Shell decalcified at margin, body intact |
| 895a | — | MCZ 297601 | 4.2 × — × 1.0 | Shell sides broken, margin decalcified, body intact |
| 895b | — | LACM 2357a | 4.6 × — × 1.5 | Shell sides broken, margin decalcified, body intact |
| 895c | — | LACM 2357b | — — — | 1 decalcified juvenile under 1 mm |
| 896 | — | MCZ 297062 | — — — | 3 decalcified juveniles under 1 mm |
| 984a | 7A–E | USNM859970 | 5.2 × 3.7 × 1.2 | Holotype, shell dry, body sectioned (female) |
| 984b | — | USNM 859971 | 4.5 × — × — | Shell sides and apex broken, body intact |
| 984c | 11B | LACM 2358 | 4.0 × 3.0 × 1.3 | Shell broken, radula used |
| 989 | — | LACM 2359 | — — — | Shell only, broken |
| 991 | 7F–H | LACM 2360 | 4.5 × 3.0 × 1.0 | Shell margin decalcified, body intact |
| 82-36a | 8A–D, 11C–E | MNHN — | 3.2 × 2.3 × 1.2 | Shell dry (4 separate bodies, radula used) |
| 82-36b | — | MNHN — | — — — | Shell dry, anterior end broken |
| 82-36c | — | MNHN — | — — — | Shell fragmented, dry |
| 1221a | 8E–H | LACM 2361a | 3.9 × 2.7 × 0.8 | Shell intact, body intact |
| 1221b | — | LACM 2361b | 1.8 × 1.3 × 0.6 | Shell intact, body intact |
| 1222 | — | USNM 859972 | 1.6 × 1.2 × 0.6 | Shell intact, body intact |
| 1223 | — | USNM 859973 | — — — | Juvenile, shell decalcified |
| 1226a | 9D–F | — — | 0.9 × 0.7 × — | Turner et al., 1985, fig. 10 |
| 1226b | — | LACM 2362a | 3.6 × 2.8 × 1.1 | Shell and body intact |
| 1226c | — | LACM 2362b | — — — | Shell and body crushed, ca. 4 mm long |
| 1226d | — | LACM 2362c | 2.5 × 1.9 × 0.7 | Shell decalcified, body intact |
| 1226e | — | LACM 2362d | — — — | 2 small crushed, 2 decalcified juveniles under 1 mm |
| 1226f | — | USNM 859974a | 3.2 × 2.2 × 1.1 | Intact, partially decalcified at margin |
| 1226g | — | USNM 859974b | 2.6 × 2.0 × 1.0 | Intact, partially decalcified at margin |
| 1226h | — | USNM 859974c | 2.5 × 1.8 × 0.8 | Intact, partially decalcified at margin |
| 1226i | — | USNM 859974d | 1.8 × 1.3 × 0.5 | Intact, partially decalcified at margin |
| 1226j | — | USNM 859974e | 1.7 × 1.2 × 0.5 | Intact, partially decalcified at margin |
| 1226k | — | MCZ 297063a | 3.1 × 2.3 × 0.9 | Intact, partially decalcified at margin |
| 1226l | — | MCZ 297063b | 2.3 × 1.5 × 0.7 | Intact, partially decalcified at margin |
| 1226m | — | MCZ 297063c | 2.0 × 2.6 × 0.6 | Intact, partially decalcified at margin |

Table 2. Continued.

| Dive | Figure | Museum no. | Dimensions (mm) | Condition |
|---|---|---|---|---|
| 1226n | — | MCZ 297063d | 1.6 × 1.1 × 0.4 | Intact, partially decalcified at margin |
| 1226o | — | MCZ 297063e | 1.3 × 1.0 × 0.3 | Intact, partially decalcified at margin |
| | | | *Clypeosectus curvus* | |
| 1494 | — | USNM 859975 | 4.1 × 3.2 × 1.8 | Shell chipped, body used for radular attempt |
| 1447 | 10G, 11F | LACM 2363 | 2.4 — — | Shell fragmented, body used for radula |
| 1729 | — | MCZ 297064 | 4.8 × 3.7 × 2.0 | Shell only, chipped near slit |
| 1730a | 10A–F | USNM 859976 | 4.6 × 4.0 × 2.0 | Holotype, shell dry, body intact |
| 1730b | 10H | LACM 2364a | 4.0 × 3.5 × 2.0 | Shell dry, body sectioned (female) |
| 1730c | — | LACM 2364b | 4.4 × 3.8 × 2.0 | Shell dry, chipped, body sectioned (male) |
| 1730d | — | LACM 2364c | — — — | Shell fragments, radular attempt |
| 1730e | — | LACM 2364d | 3.4 × 2.4 × 1.6 | Shell only, edges chipped |
| 1733 | — | LACM 2365 | 2.3 × 1.9 × 0.6 | Shell margin decalcified, body intact |
| | | | *Pseudorimula marianae* | |
| 1836a | 12A–E, 13C,D | USNM 859977 | 6.4 × 5.2 × 2.4 | Holotype, shell dry, radula used, body sectioned (female) |
| 1836b | 12F | LACM 2366a | 8.6 × 7.1 × 3.3 | Shell dry, edges broken, body sectioned (male) |
| 1836c | — | USNM 859978 | 6.1 × 4.9 × 2.5 | Shell dry, body intact |
| 1836d | 12G,H | LACM 2366b | 4.1 × 3.1 × 1.7 | Shell in good condition, body intact |
| 1843 | 13A,B | LACM 2367 | 2.7 × 2.0 × 0.8 | Shell scanned, body intact |

eral teeth three pairs, each with four denticles; basal part of shafts of laterals and inner marginal teeth fading into basal membrane of ribbon.

**REMARKS.** This genus is based on a single, previously unfigured species from the hydrothermal vents of the Juan de Fuca Ridge.

**ETYMOLOGY.** The generic name is a Greek compound of *temno,* to cut, and *kinklis,* lattice, suggested by the sculpture and deeply cut slit. Gender: feminine.

## *Temnocinclis euripes* new species

Figures 1A–H, 4A, 5A,B

Split limpet; Tunnicliffe, 1988:353.

**DIAGNOSIS.** Shell asymmetical, apical whorl projecting posteriorly, sculpture clathrate.

**DESCRIPTION.** Shell (Figs. 1A–C,G,H, 4A) large for family (maximum length 4.0 mm), thin; periostracum thick, light brown; outline of aperture elongate oval, anterior broader than posterior, margin of aperture in same plane; apical whorl (first whorl of teleoconch) projecting posteriorly. Profile relatively high; height of holotype 0.39 times length. Protoconch diameter 250 μm, surface sculpture unknown (all specimens coated, Fig. 4A). First whorl of teleoconch rounded, descending below protoconch; sculpture weak, both axial and spiral. Slit arising at position of three-fourths growth of first teleoconch whorl, at which stage aperture expands to produce limpet form through one-half whorl of additional rotation. Slit open more than half length of shell in dorsal view, dividing shell into nearly equal areas, its position only slightly deflected to right in dorsal view. Slit-borders sharply raised, edges enveloped by periostracum; left and right sides of shell with interlocking projections along anterior termination of slit (Fig. 1G). Selenizone depressed below slit-borders, filled with fine lamellar additions. Sculpture of sharply raised axial ribs and spiral cords, forming laterally stretched beads at intersections. Additional spiral cords arising in interspaces, assuming equal prominence so that overall number of beaded intersections increases with growth while strength of beading remains the same. Apertural lip thin anteriorly, posteriorly forming broad, depressed shelf in position corresponding to columella. Periostracum stretched across depression of posterior shelf (Figs. 1B,H). Muscle scar barely detectable, its terminations rounded, extending anteriorly to position equal to greatest breadth of shell. Shell interior highly transparent, revealing exterior clathrate sculpture except near margin, where surface is somewhat opaque. Slit-border and previous positions of septum not marked by heavy deposition of interior callus.

**External Anatomy** (Figs. 1D–F,H). Cephalic tentacles non-papillate, thick, short (contracted condition); three posterior pairs of non-papillate epipodial tentacles. Shell muscle horseshoe-shaped, solid, muscle terminations rounded. Two monopectinate ctenidia, left slightly larger than right. Foot with double anterior edge marking opening of pedal gland; operculum attached to metapodium, multispiral with early volutions raised (Figs. 1F,H).

Internal anatomy is described by Haszprunar, (1989).

**Radula** (Figs. 5A,B). Radular ribbon nearly symmetrical. Rachidian tooth broad, with strong lateral

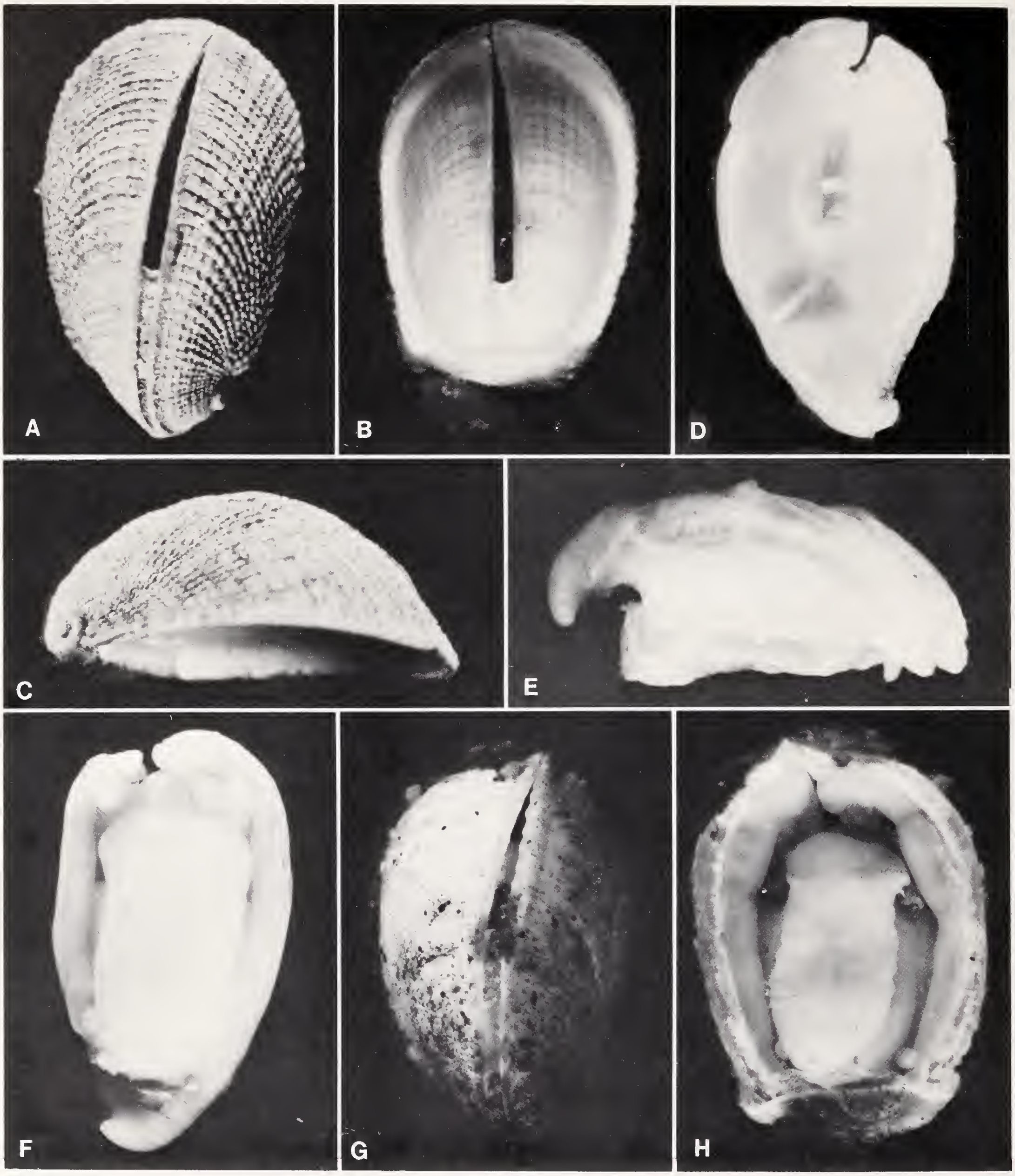

**Figure 1.** *Temnocinclis euripes,* shell and external anatomy. Anterior at top in dorsal and ventral views. **A–C.** USNM 859964, holotype. Axial Seamount, Juan de Fuca Ridge, *Pisces IV* dive 1726. Length 3.8 mm. **A.** Exterior view. **B.** Interior, showing band of periostracum across posterior margin. **C.** Right side. **D.** LACM 2353a, body of paratype, dorsal view. Southern Juan de Fuca Ridge, *Alvin* dive 1463. Length 3.4 mm. **E,F.** LACM 2351, body of paratype, prior to sectioning. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1447. **E.** Right side showing monopectinate right ctenidium. **F.** Ventral view, showing operculum attached to metapodium. **G,H.** LACM 2352a, paratype with attached body, showing less pronounced sculpture and decalcification at margin. Axial Seamount, Juan de Fuca Ridge, *Alvin* dive 1726. Length 4.0 mm. **G.** Dorsal view. **H.** Ventral view, showing attached operculum.

projections, overhanging edge with sharp pointed central cusp, flanked by five to six pairs of smaller pointed cusps. Three pairs of lateral teeth with similar morphology, overhanging cusps with four sharp denticles, decreasing in size from large innermost cusp; shafts of laterals with elbows corresponding to lateral projections of rachidian; shafts below elbow fading into basal membrane of ribbon. Enlarged outer lateral and lateromarginal plate lacking. Marginal teeth numerous, cusps of similar size and with four pointed denticles like those of laterals; shafts of innermost marginals short, fading into basal membrane in manner like that of laterals; shafts of outer marginals long, not clearly separated at base from those of adjacent marginals.

**DIMENSIONS.** Length 3.8, width 2.4, height 1.5 mm (holotype).

**TYPE LOCALITY.** Hydrothermal vents of Axial Seamount, Juan de Fuca Ridge off Washington (45°59.5′N, 130°03.5′W), 1575 m.

**TYPE MATERIAL.** Holotype and three paratypes from *Pisces IV* dive 1726, 27 July 1986. Holotype, USNM 859964 (Figs. 1A–C). Paratypes from this dive and other dives from the Endeavour Segment, Juan de Fuca Ridge, and other sites on the southern Juan de Fuca Ridge are distributed as indicated in Tables 1 and 2.

The holotype shell is the only specimen in good condition; it is preserved dry and the body has been sectioned. All specimens except the holotype exhibit some decalcification at the margin. No juvenile specimens smaller than a length of 1.8 mm are known.

**DISTRIBUTION.** Hydrothermal-vent community at Juan de Fuca Ridge, from northern Endeavour Segment (47°57.0′N) to southern section (44°39.2′N).

**REMARKS.** Sculpture ranges from sharply clathrate (holotype, Figs. 1A,C) to very weak (Fig. 1G). Of the present material, the holotype has the best-developed sculpture.

**ETYMOLOGY.** The specific name of the type species, from Greek *euripos,* means strait, or channel, referring to the slit.

## *Temnozaga* new genus

**TYPE SPECIES.** *Temnozaga parilis* new species.

**DESCRIPTION.** Shell elongate, relatively high; apical whorl close to apertural margin. Protoconch sculpture smooth with fine reticulations. Sculpture predominantly radial, concentric sculpture of raised lamellae. Slit-borders raised, with interlocking projections in contact at anterior end. Columella with angular posterior ridge.

**External Anatomy.** Cephalic tentacles and ctenidia as diagnosed for subfamily. Four posterior pairs of epipodial tentacles. Operculum small, multispiral, edges of early volutions raised. Ctenidia monopectinate.

**Radula.** Rachidian broad, overhanging tip narrow, with three main cusps, three pairs of lateral teeth, each with four denticles; basal part of shafts of laterals and inner marginals fading into basal membrane of ribbon.

**REMARKS.** This genus is based on a single, previously figured species from hydrothermal vents at 21°N on the East Pacific Rise.

*Temnozaga* and *Temnocinclis* share a number of features, including relatively large size for the family, the interlocking projections of the shell edge along the anterior contact, and similar opercular morphology. There are, however, two major differences: the position of the apex, posterior to the shell margin in *Temnocinclis,* but not in *Temnozaga,* and, of more importance, the excavated posterior rim in *Temnocinclis,* over which the periostracum extends. There is no comparable structure in *Temnozaga,* which has a smooth posterior rim. There are also major differences in the radula: the rachidian and lateral teeth of *Temnocinclis* have more secondary cusps than those of *Temnozaga, Temnozaga* has a much narrower overhanging cusp on the rachidian tooth, and the innermost marginal teeth of *Temnozaga* have longer shafts than those of *Temnocinclis.*

**ETYMOLOGY.** The generic name is a Greek compound of *temno,* to cut, and part of zig-zag, with reference to the deeply cut slit and the interlocking projections of the shell along the slit margin anteriorly. Gender: neuter.

## *Temnozaga parilis* new species

Figures 2A–H, 4B,C, 5C,D

Unnamed *Rimula*(?); Turner, Lutz, and Jablonski, 1985, figs. 11a–c (juvenile shell and protoconch).

**DIAGNOSIS.** Shell nearly symmetrical, apical whorl not projecting.

**DESCRIPTION.** Shell (Figs. 2A–C, 4B,C) relatively large for family (maximum length 4.0 mm); periostracum thick; outline of aperture elongate-oval, broader anteriorly. Margin of aperture nearly in same plane, sides raised slightly relative to ends. Highest elevation of shell at half its length. Profile moderately high, height of holotype 0.41 times length. Apical whorl nine-tenths shell length from anterior end, deflected to right. Protoconch diameter 170 μm; protoconch surface smooth; first teleconch whorl smooth, rounded, slightly descending below level of protoconch, slit arising three protoconch diameters away at position of one-half whorl of growth in first teleoconch whorl, at which stage expansion of aperture produces limpet form through one-half whorl of additional rotation. Slit open nearly three-fourths length of shell in dorsal view, not deflected to right. Slit-borders sharply raised, bearing alternating, interlocking projections in contact anteriorly. Selenizone depressed below slit-border, additions to selenizone slightly curved, projecting farther anteriorly on left side. Sculpture of about 30 strong primary ribs with one to three secondary and tertiary ribs arising in interspaces. Concentric sculpture of fine growth lines, raised into sharp lamellar scales on crossing primary radial ribs. Shell margin finely crenulated by ribs. Apertural lip thin anteriorly, forming angulate ridge posteriorly in position corresponding to columella. Shell interior opaque white, muscle scar barely detectable, its terminations rounded. Slit bordered by slightly raised callus deposition.

**External Anatomy** (Figs. 2D–H). Body nearly bilaterally symmetrical; cephalic tentacles thick, tapered, short (contracted condition); four posterior pairs of epipodial tentacles (strongly contracted),

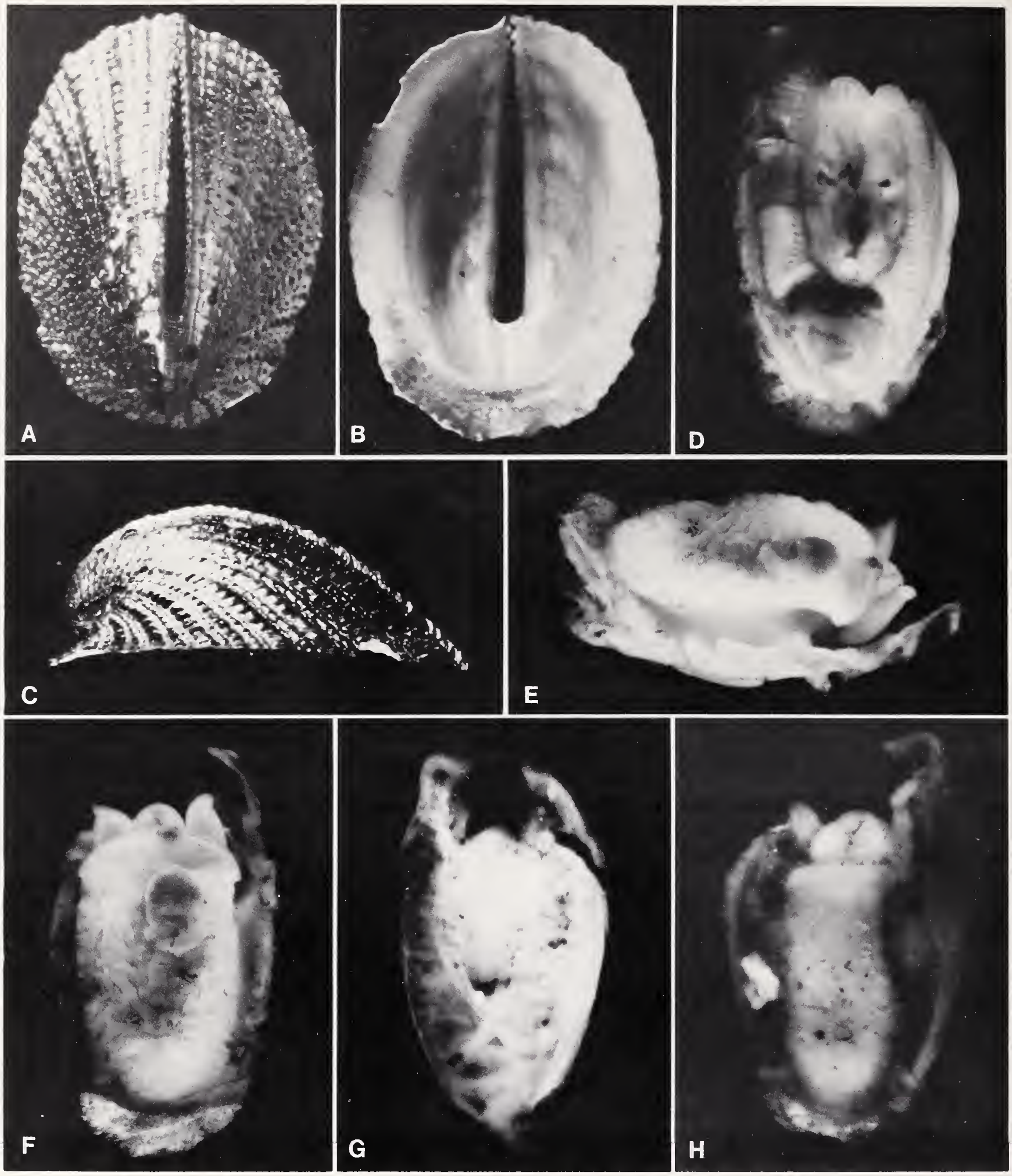

**Figure 2.** *Temnozaga parilis,* shell and external anatomy. East Pacific Rise at 21°N. Anterior at top in dorsal and ventral views. **A–C.** USNM 859966, holotype shell, photographed subsequent to gold coating for scanning and loss of pieces of periostracum. *Alvin* dive 1226. Length 4.0 mm. **A.** Exterior view. **B.** Interior view. C. Right side. **D–F.** Body of holotype prior to sectioning, mantle skirt torn away anteriorly. Length 2.5 mm. **D.** Dorsal view, showing paired monopectinate ctenidia by transparency through mantle skirt. **E.** Left side, showing folded operculum. **F.** Ventral view, showing inner side of iridescent operculum. **G,H.** LACM 2354, body of paratype (shell lost), prior to extraction of radula. *Alvin* dive 1229. Length 1.0 mm. **G.** Dorsal view, showing paired monopectinate ctenidia by transparency through mantle skirt. **H.** Ventral view, showing operculum and paired epipodial tentacles at posterior end of foot.

decreasing in size posteriorly, all tentacles non-papillate. Shell muscle horseshoe-shaped, of similar width throughout; muscle terminations rounded. Two monopectinate ctenidia of equal size, 27 leaflets visible on left ctenidium (right ctenidium damaged). Foot with double anterior edge marking opening of pedal gland. Operculum 1.3 mm in diameter, at least six volutions, edges of early volutions raised (Figs. 2E,F).

**Radula** (Figs. 5C,D). Radular ribbon slightly asymmetrical. Rachidian tooth broad, its basal area expanded, neck of overhanging tip narrow, with

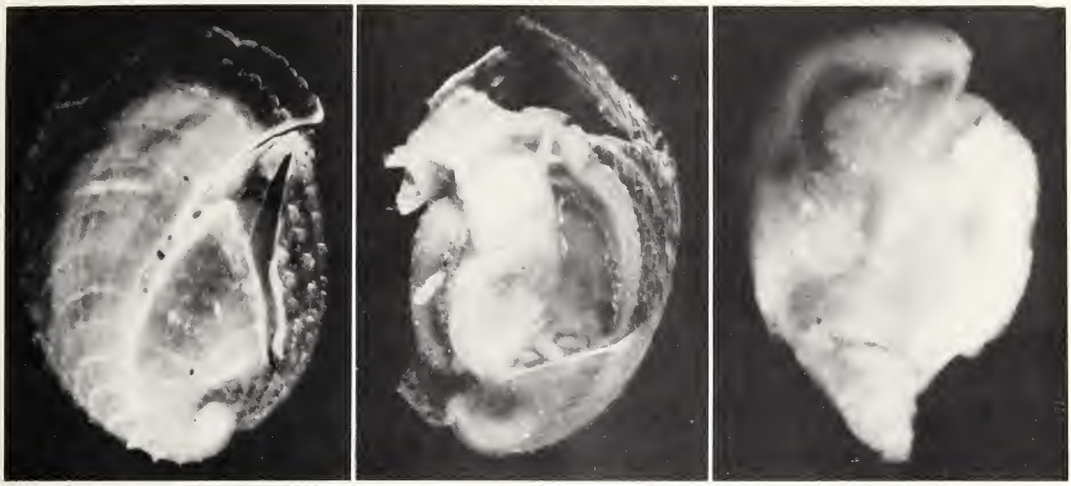

**Figure 3.** *Sutilizona theca,* shell and external anatomy. East Pacific Rise at 12°N. Anterior at top in dorsal and ventral views. **A,B.** LACM 2355a, paratype with body attached, prior to sectioning. *Alvin* dive 2003. Length 1.3 mm. **A.** Dorsal view. **B.** Ventral view. **C.** USNM 859966, holotype body prior to sectioning, showing monopectinate ctenidia by transparency, the left larger than the right. *Alvin* dive 2003. Length 1.2 mm.

sharp pointed central cusp, flanked by one relatively large cusp on either side, sometimes with smaller cusps between. Three pairs of similar lateral teeth, overhanging edge with one major cusp and one or two minor cusps; shafts of laterals with elbows corresponding to basal projections of rachidian; shafts below elbow fading into basal membrane of ribbon. Enlarged outer lateral and lateromarginal plate lacking. Marginal teeth numerous, cusps of similar size and with denticles like those of laterals, shafts with strong indentation near tip; shafts of all marginals long, those of outermost marginals not clearly separated from those of adjacent marginals.

**DIMENSIONS.** Length 4.1, width 3.0, height 1.7 mm (holotype).

**TYPE LOCALITY.** East Pacific Rise at 21°N (20°50.0′N, 109°06.0′W), 2616 m.

**TYPE MATERIAL.** Holotype from *Alvin* dive 1226, 10 May 1982. Holotype, USNM 859966. The shell had been coated with gold for SEM by R. Lutz (Figs. 4B,C) prior to photography (Figs. 2A–C), which accounts for its present metallic appearance. The holotype body (Figs. 2D–F) has been sectioned by Haszprunar; the operculum remains intact. Paratype (LACM 2354, Figs. 2G,H) from *Alvin* dive 1229, single body 1.0 mm long of which the anterior end was used for the radular preparation; the posterior part of the body with operculum attached remains.

**DISTRIBUTION.** Hydrothermal-vent habitat of East Pacific Rise at 21°N.

**REMARKS.** The imbricate sculpture on the radial ribs resembles that of the clypeosectid *Pseudorimula marianae* new species, but that represents convergence in shell characters between two families in different superfamilies. Differences from *Temnocinclis euripes* are treated above.

**ETYMOLOGY.** The specific name is Latin for equal, denoting the symmetry of the teleoconch shell.

## SUTILIZONINAE new subfamily

**TYPE GENUS.** *Sutilizona* new genus.

**DESCRIPTION.** Shell of strongly asymmetrical limpet form, retaining a coiled portion; slit closed (fused) at maturity. Protoconch reticulate with deep pits. Radula lacking enlarged fourth lateral tooth, marginal teeth similar to lateral teeth. Ctenidia monopectinate, of unequal shape and position; cephalic and epipodial tentacles non-papillate, eyes lacking.

For anatomical characters see Haszprunar (1989).

**REMARKS.** Although the new genus *Sutilizona* has monopectinate ctenidia, as do both genera of the new subfamily Temnocinclinae, additional characters of the protoconch and radula are unique to it, and are not represented in any other genus of Scissurellidae. Haszprunar (1989) finds further justification for separating this genus at the subfamily level.

In shell characters *Sutilizona* is unlike *Temnocinclis* and *Temnozaga* in having no posterior ridge for muscle insertion on the shell interior, in retaining a posterior coiled portion visible on the interior side, and in having the slit sealed anteriorly in mature specimens. The anteriorly sealed slit is a character shared with the shallow-water scissurellid genera *Sinezona* (subfamily Scissurellinae) and *Sukashitrochus* (subfamily Anatominae), each of which is assigned to a different subfamily on the basis of radular and protoconch characters.

The radula of *Sutilizona* is more similar to that of *Temnozaga* than to *Temnocinclis* in having a

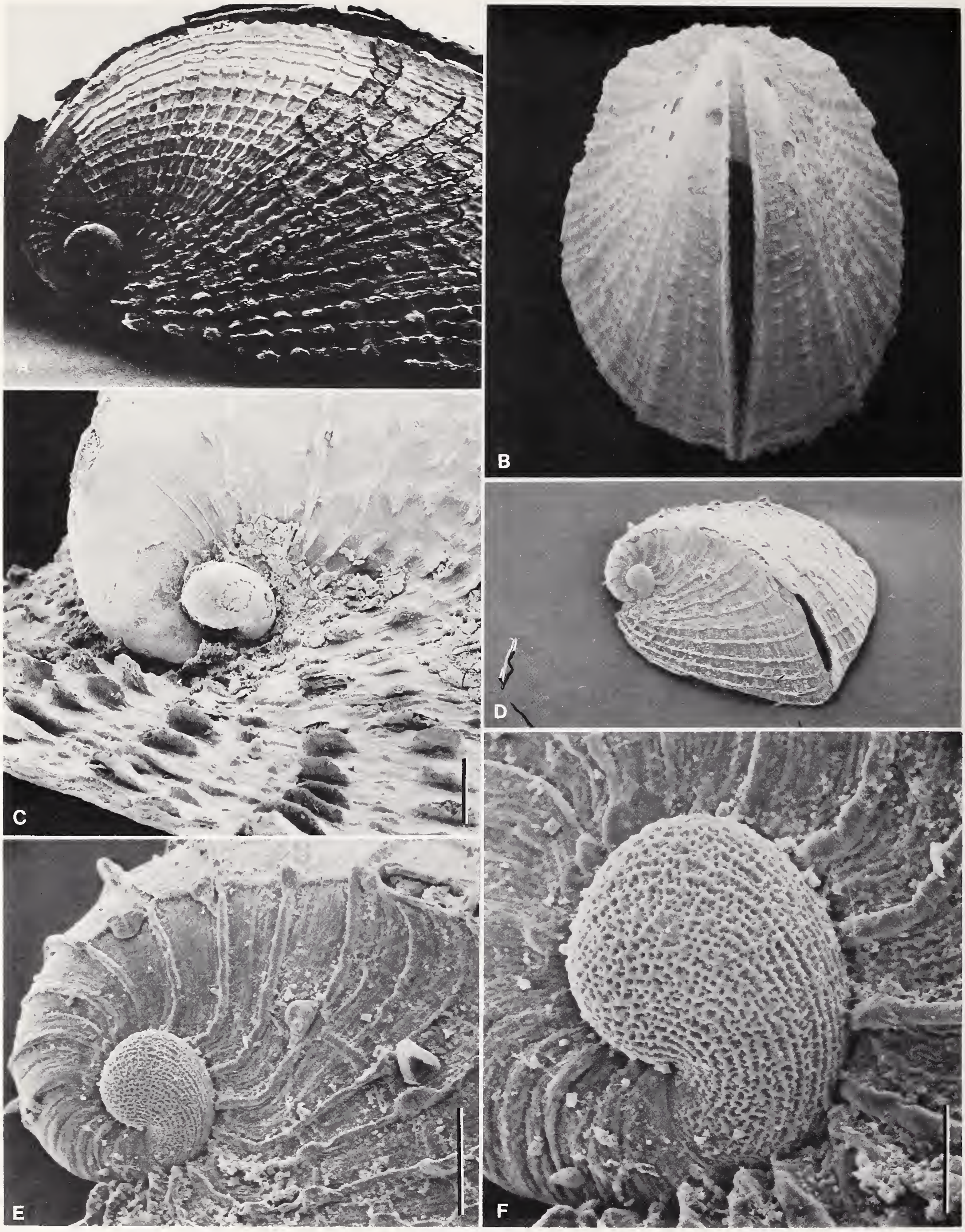

**Figure 4.** SEM views of early sculpture and protoconchs of scissurellids from hydrothermal vents. **A.** *Temnocinclis euripes.* LACM 2352b, right lateral view of paratype, in which surface of protoconch has exfoliated. Axial Seamount, Juan de Fuca Ridge, *Pisces IV* dive 1726. Length 2.7 mm. **B,C.** *Temnozaga parilis.* USNM 859966, holotype shell (after Turner et al., 1985, figs. 11a,b). East Pacific Rise at 21°N, *Alvin* dive 1226. Length 4.0 mm. **B.** Exterior view, anterior at bottom. C. Enlarged view of apical area showing lamellar sculpture and eroded protoconch. Scale bar = 100 μm. **D–F.** *Sutilizona theca.* USNM 859967, holotype shell. East Pacific Rise at 13°N, *Alvin* dive 2003. Length 1.3 mm (anterior end broken). **D.** Oblique view of entire shell from left side (anterior end broken to left of foramen). Scale bar = 400 μm. **E.** Protoconch and early teleoconch sculpture. Scale bar = 100 μm. **F.** Enlarged view of protoconch showing pits. Scale bar = 40 μm.

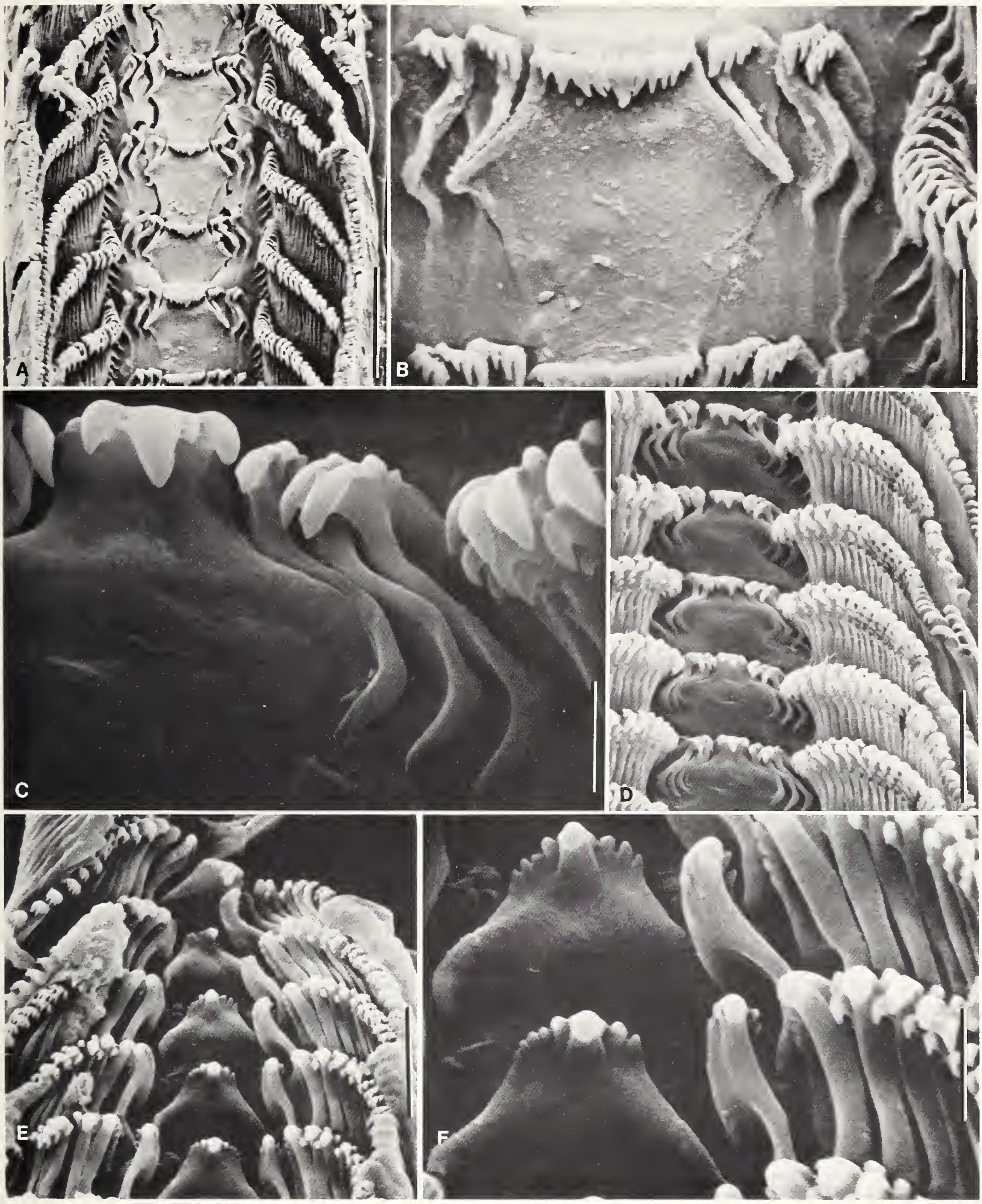

**Figure 5.** SEM views of radulae of hydrothermal-vent scissurellids. **A,B.** *Temnocinclis euripes.* USNM 859963. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1452. **A.** Full width of radular ribbon. Scale bar = 40 μm. **B.** Rachidian, three pairs of laterals, and inner marginals. Scale bar = 10 μm. **C,D.** *Temnozaga parilis.* LACM 2354. East Pacific Rise at 21°N, *Alvin* dive 1229. C. Rachidian, laterals, and tips of inner marginals. Scale bar = 4 μm. **D.** Half width of ribbon. Scale bar = 20 μm. **E,F.** *Sutilizona theca.* LACM 2355b. East Pacific Rise at 13°N, *Alvin* dive 2003. **E.** Full width of ribbon. Scale bar = 10 μm. **F.** Rachidian, laterals, and inner marginals. Scale bar = 4 μm.

narrower overhanging cusp and relatively few secondary cusps on the rachidian and lateral teeth. It differs primarily in the lack of morphological distinction between lateral and marginal teeth, making it unclear whether there are two or three pairs of lateral teeth. Marginal teeth of *Temnozaga* (Fig. 5C) may be distinguished from lateral teeth in having a significant indentation high on the shaft, but there is no indentation on the marginals of *Sutilizona.*

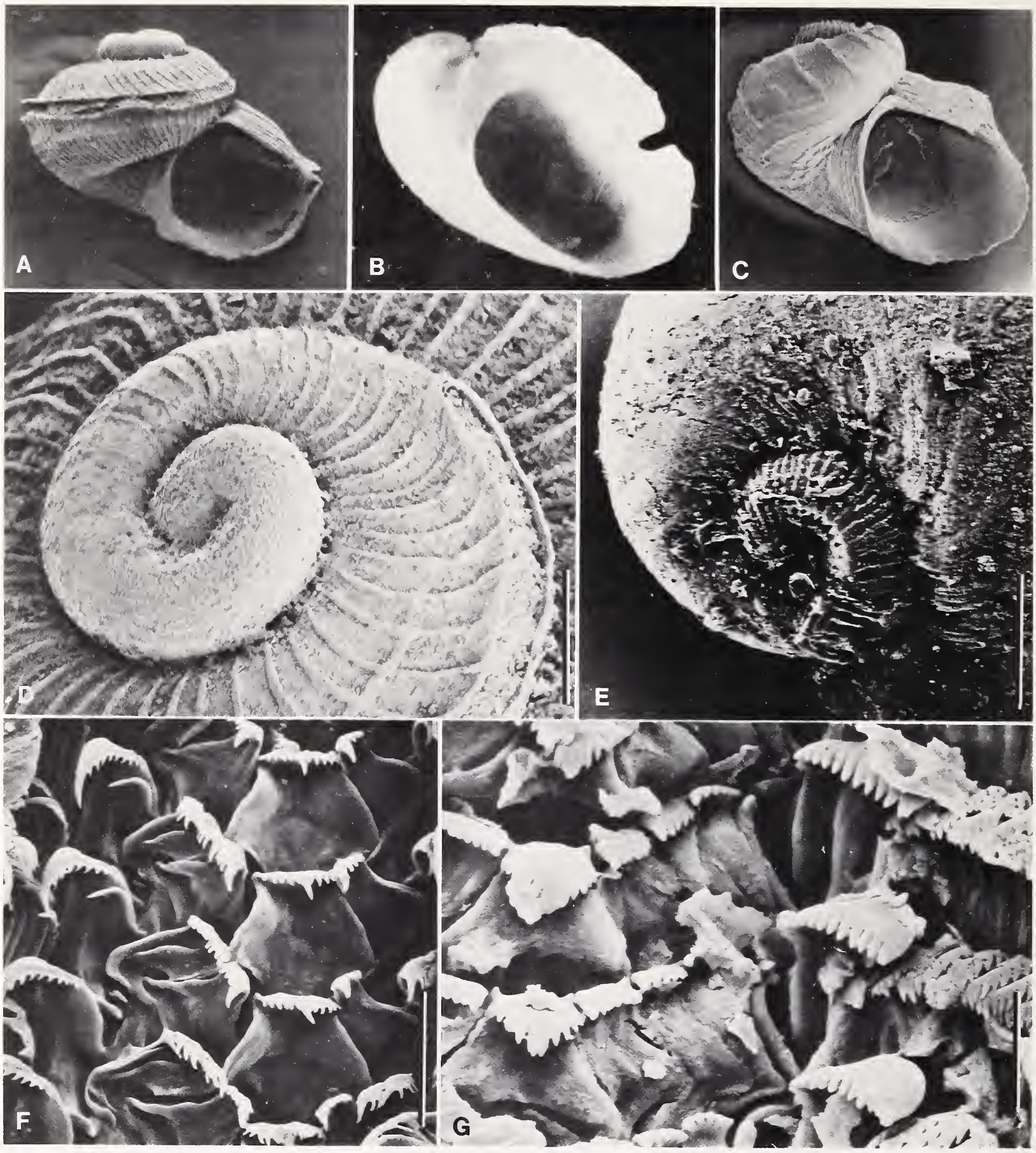

**Figure 6.** SEM views (except B) of shells, protoconchs, and radulae of non-hydrothermal vent scissurellids. **A.** Shell of *Anatoma lyra* (Berry, 1947). LACM 82-64. Cordell Bank, California, 50 m. Height 0.8 mm. **B.** Shell of *Incisura lytteltonensis* (E.A. Smith, 1894). LACM 47-3. Stewart Island, New Zealand. Length 1.3 mm. **C.** Shell of *Sinezona rimuloides* (Carpenter). LACM 66-57. Carmel, California. Height 0.8 mm. **D.** Protoconch of *Anatoma lyra,* showing smooth surface with irregular reticulation. Same specimen as in Figure 6A. Scale bar = 100 μm. **E.** Protoconch of *Incisura lytteltonensis,* showing strong axial ridges. Same lot as Figure 6B. Scale bar = 100 μm. **F.** Radula of *Anatoma crispata* (Fleming, 1832), showing rachidian (right center) and four pairs of laterals, the enlarged outermost (at left) with pointed tip and serrations on inner side. Scale bar = 20 μm. **G.** Radula of *Incisura lytteltonensis,* showing rachidian (at left) and four pairs of laterals, the enlarged outermost (at right) with numerous strong serrations on inner side. Scale bar = 10 μm.

## *Sutilizona* new genus

**TYPE SPECIES.** *Sutilizona theca* new species.

**DESCRIPTION.** Shell oval and relatively low; apical whorl sharply offset to right and directly above posterior margin. Protoconch with deep pits. Sculpture predominantly concentric, radial sculpture suggested by linear alignment of raised lamellae. Slit-borders not raised, slit sealed anteriorly. Shell interior retains coiled portion at posterior.

**External Anatomy.** Cephalic and epipodial tentacles non-papillate, epipodial tentacles one posterior pair. Operculum small. Ctenidia monopectinate, unequal.

**Radula.** Rachidian tooth broad at base, overhanging tip narrow; with one prominent and two to four smaller cusps; lateral teeth at least two pairs, of similar morphology as marginal teeth.

**REMARKS.** This genus is based on a single species from hydrothermal vents at 12°N on the East Pacific Rise.

**ETYMOLOGY.** The generic name is a compound of the Latin *sutilis,* sewn together, and Latin *zona,* belt, referring to the sealed selenizone of mature specimens. Gender: feminine.

### *Sutilizona theca* new species

Figures 3A–C, 4D–F, 5E,F

**DIAGNOSIS.** Slit closed at maturity, shell retaining coiled portion.

**DESCRIPTION.** Shell (Figs. 3A,B, 4D–F) small for family (possibly immature), maximum length 1.3 mm; periostracum thin; outline of aperture oval, broader anteriorly. Apical whorl deflected to right and overhanging posterior margin; protoconch diameter 250 $\mu$m; protoconch sculpture drawn into elongate rows with deep pits. First teleoconch whorl rounded, with strong collabral (axial) ribs; slit arising two protoconch diameters away at position of three-fourths whorl of growth in first teleoconch whorl, at which stage expansion of aperture produces limpet form. Slit sealed anteriorly at shell length of 0.9 mm, open only one-fourth length of shell in dorsal view, slit and selenizone strongly curved to right. Slit-borders not sharply raised; selenizone not depressed below slit-border. Spiral sculpture weak except for one strong rib arising at one-half whorl of growth in first teleoconch whorl and extending to slit-band. Concentric sculpture strong, producing raised lamellar scales on crossing weak radial sculpture. Apertural lip thin and fragile. Shell interior transparent, muscle scar not deeply impressed, slit and selenizone bordered by raised ridges of callus. Shell interior retaining coiled portion posteriorly.

**External Anatomy** (based on 1.3 and 1.1 mm bodies; Figs. 3B,C). Body asymmetrical; cephalic tentacles slender, moderately long (contracted condition); one posterior pair of epipodial tentacles. Shell muscle horseshoe-shaped, longer on left side, muscle terminations expanded inwardly. Left ctenidium monopectinate, up to seven leaflets visible through transparent mantle skirt in larger specimen, four in smaller specimen. Right gill not visible through mantle. Foot with double anterior edge marking opening of pedal gland. Operculum small, nearly transparent, diameter about 0.5 mm in larger specimen.

Internal anatomy is described by Haszprunar (1989).

**Radula** (Figs. 5E,F). Radular ribbon symmetrical. Rachidian tooth broad, its basal area expanded, neck of overhanging tip narrow, with sharp pointed central cusp, flanked by two to four smaller irregular cusps. Lateral teeth at least two pairs, each with large main cusp and one to two smaller cusps on each side; first lateral with depression on front surface to fit edge of rachidian; second lateral similarly shaped to fit against first lateral. Shafts of lateral teeth and marginal teeth long, their bases concealed by cusps of row below. Third and subsequent teeth in row not clearly distinguishable as either laterals or marginals.

**DIMENSIONS.** Length 1.1 (shell anterior broken, projected length 1.3), width 0.9, height 0.5 mm (holotype).

**TYPE LOCALITY.** On sulfide mounds at base of inactive chimney, East Pacific Rise near 12°N (11°46′N, 103°47′W), 2715 m.

**TYPE MATERIAL.** Holotype and two paratypes from *Alvin* dive 2003, 25 March 1988. Holotype, USNM 859967; two paratypes, LACM 2355 (Tables 1, 2). All specimens are in damaged condition. The holotype (Figs. 4D–F) has been coated for SEM and the body removed for sectioning. One paratype (Figs. 3A,B), initially broken, has been separated from the shell for sectioning, resulting in further breakage. The third paratype was initially so decalcified that nothing but shell fragments remain; the body was used for radular extraction.

**DISTRIBUTION.** Hydrothermal vents of East Pacific Rise near 12°N.

**REMARKS.** It is possible that the present specimens are immature, considering that their ctenidia are so poorly developed: one specimen showed seven leaflets and the other four on the left ctenidium. However, the closed slit seems to suggest that the specimens may be mature. In *Sinezona* (subfamily Scissurellinae) the slit is open during most of the growing phase and is closed only at maturity.

**ETYMOLOGY.** The specific name *theca* is Latin, sheath, a feminine noun in apposition referring to the coiled portion of the shell that is retained in the interior (ventral) view.

## Superfamily FISSURELLACEA Fleming, 1822

## CLYPEOSECTIDAE new family

**TYPE GENUS.** *Clypeosectus* new genus.

**DESCRIPTION.** Shell of limpet form with deep, asymmetrical slit or foramen; slit-borders raised, nearly in contact or sealed at anterior end. Apex deflected to right, not overhanging posterior margin. Shell lacking pits (or pores) on early teleoconch. Muscle scar without inturned hooked-process of fissurellids; anterior extension of pallial attachment scar producing false muscle scar.

**External Anatomy.** Eyes lacking, cephalic tentacles not papillate. Epipodial tentacles not papil-

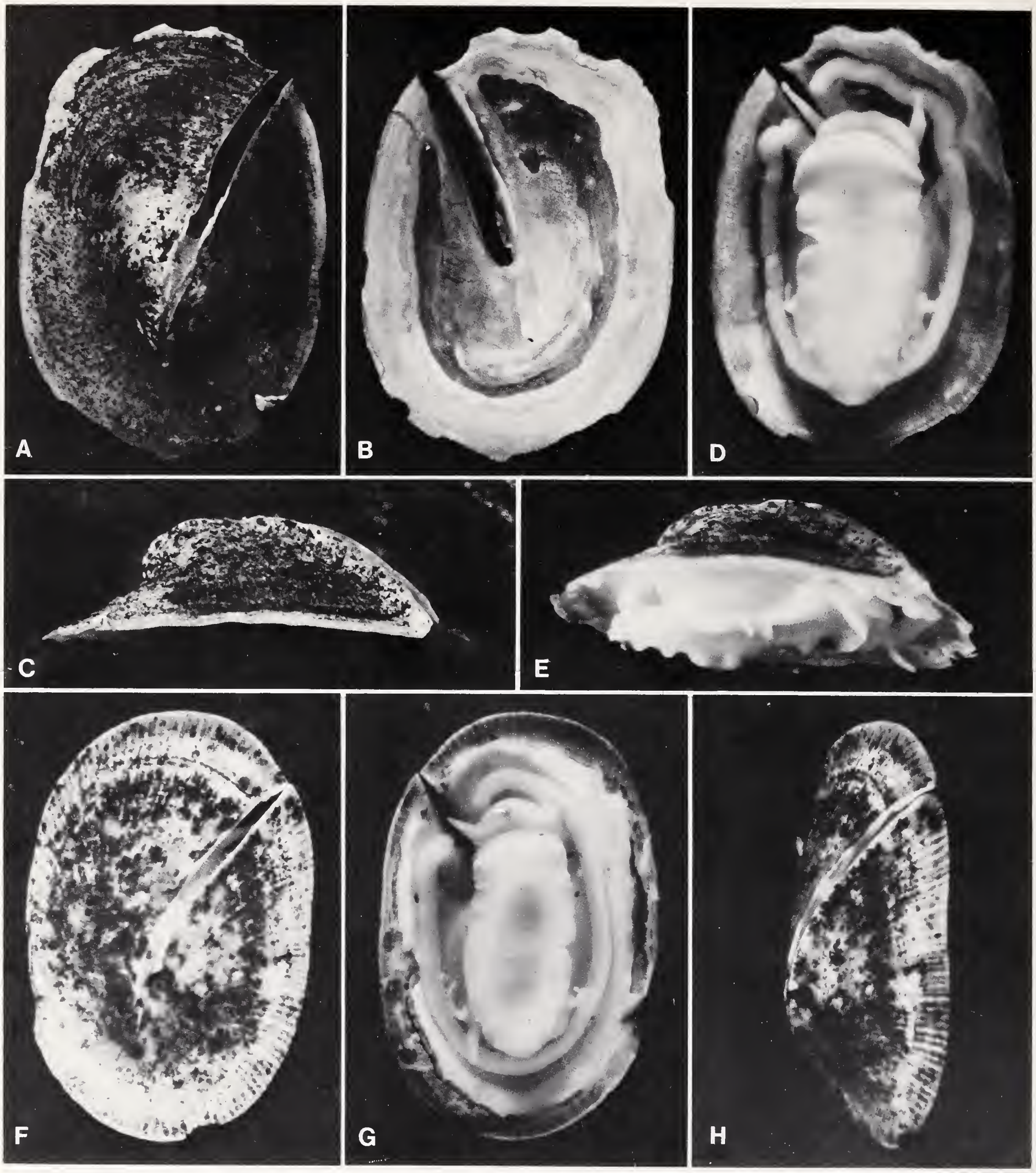

Figure 7. *Clypeosectus delectus,* shell and external anatomy of specimens from Galapagos Rift. Anterior at top in dorsal and ventral views. **A–E.** USNM 859970, holotype. *Alvin* dive 984. Length 5.2 mm. **A.** Exterior surface with black mineral deposits. **B.** Interior, showing forward extension of muscle scar produced by pallial attachment scar. **C.** Right side showing elevated slit-border. **D.** Ventral view showing right tentacle projecting through slit. **E.** Oblique view from right side. **F–H.** LACM 2360, paratype. *Alvin* dive 991. Length 4.5 mm. **F.** Exterior, surface encrusted with black mineral deposits. **G.** Ventral view with body attached. **H.** Oblique view of right side.

late, three posterior pairs in *Clypeosectus,* four posterior pairs plus two anterior pairs in *Pseudorimula.* In *Clypeosectus* both sexes with small genital process at ventral base of right cephalic tentacle and ciliated band along right neck (Haszprunar, 1989). Foot with double anterior edge marking opening of pedal gland. Paired ctenidia bipectinate, right ctenidium smaller than left. Operculum lacking at maturity. Shell muscle without hooks.

For anatomical characters see Haszprunar (1989).

**Radula.** Radular ribbon nearly symmetrical. Rachidian tooth with long, tapering overhanging tip, edges with strongly projecting serrations; shaft of rachidian broad at base. Lateral teeth five to nine pairs, overhanging tips decreasing gradually in size away from rachidian, similar in morphology to rachidian, with strongly projecting serrations; shafts of laterals long and narrow, outermost laterals with longer, more sinuous shafts. Enlarged outer lateral tooth lacking. Marginal teeth numerous, with spatulate tips, edges finely and sharply serrated, serrations similar to those of laterals. Marginals and outer laterals with one long denticle on outer edge of shaft near overhanging tip. Marginals tending to be fused along shaft bases. Tip of each marginal in *Clypeosectus* with long, filamentous process (lacking in *Pseudorimula*).

**REMARKS.** This new family is created for the new genus *Clypeosectus,* with two species from the the eastern Pacific hydrothermal vents, and the new genus *Pseudorimula,* with one species from the western Pacific Mariana Back-Arc vents. Despite substantial differences in shell morphology and configuration of epipodial tentacles, the radular morphology of the two genera fits the same plan and confirms their affinity. Although shells of both genera resemble those of fissurellids, they differ in lacking the shell pits or pores that characterize fissurellids. The well-defined pedal gland of both genera is unknown in fissurellids.

Anatomical evidence for the establishment of a new family is given by Haszprunar (1989). Radular characters are sufficiently unique to suggest the need for a new family on this basis alone. The symmetrical radular ribbon distinguishes the clypeosectids from all fissurellids. There is no trace of the enlarged outer lateral tooth characteristic of fissurellids, which results in radular asymmetry in fissurellids. In addition, most fissurelids do not have the tendency toward similar morphology of rachidian, lateral, and marginal teeth that is exhibited by clypeosectids. The long denticle on the outer edge of the shaft of the outer lateral and marginal teeth is unique to clypeosectids. Scissurellid radulae differ principally in having a large rachidian tooth that is unlike the adjacent lateral teeth.

Due to the tendency of lateral and marginal teeth to have a similar morphology, it is difficult to distinguish between them in SEM views, and in views in which the marginals overlie the position of the laterals, it is not always possible to be certain how many lateral teeth characterize each species. Radular preparations for *C. delectus* (Figs. 8A–E) show nine pairs of lateral teeth, but only six pairs could be verified for *C. curvus* (Fig. 8F). The ninth lateral of *C. delectus* appears to be attached to a basal element that serves as a lateromarginal plate.

## KEY TO GENERA

Shell with open slit; three posterior pairs of epipodial tentacles ................ *Clypeosectus*
Slit closed at margin; two anterior pairs and four posterior pairs of epipodial tentacles .......... .............................. *Pseudorimula*

## *Clypeosectus* new genus

**TYPE SPECIES.** *Clypeosectus delectus* new species.

**DESCRIPTION.** Slit strongly deflected to right in dorsal view; slit-borders raised, nearly in contact at anterior end. Apex posterior, deflected to right, but not overhanging posterior margin. Protoconch length 200 μm, surface with finely pitted sculpture. Shell surface with thin periostracum, sculpture chiefly radial (spiral). False muscle scar produced by scar of pallial attachment extending close to border of slit anteriorly.

**External Anatomy.** Anterior end of foot broad, its tip with double anterior edge marking opening of pedal gland; foot posterior obtusely pointed; sole of foot with broad mid-ventral depressed area. Cephalic tentacles relatively long (preserved, contracted condition), the right seeming to project through slit; base of tentacle slightly enlarged in normal position of eyes. Three posterior pairs of epipodial tentacles, on body wall midway between foot edge and thick border of mantle margin. Mantle skirt deeply emarginate corresponding to slit, edge of emargination with tentaculiform appendages. Mantle skirt above head thin, nearly transparent. Shell muscle without hooks, extending anteriorly equal distances on both sides, approximately two-thirds body length. Both sexes with small genital process at ventral base of right cephalic tentacle and ciliated band along right neck. Right ctenidium smaller than left.

**Radula.** Rachidian tooth with long, tapered, overhanging tip, edges with strongly projecting serrations; shaft of rachidian broad at base. Six to nine pairs of lateral teeth, overhanging tips decreasing gradually in length away from rachidian, similar in morphology to rachidian, with strongly projecting serrations; shafts of lateral teeth long and narrow, outermost lateral with longer, more sinuous shafts. Marginal teeth numerous, with spatulate tips, edges finely and sharply serrated, serrations similar to those of lateral teeth. Marginal tooth and outer lateral tooth with one long denticle on outer edge of shaft near overhanging tip. Marginals tending to be fused along shaft bases. Tips of marginals with single long, filamentous process.

**REMARKS.** The false muscle scar produced by the anterior pallial attachment scar is more pronounced in this genus than it is in *Pseudorimula,* making the interior aspect of the shell completely unlike that of any fissurellid limpet. The radula differs from that of *Pseudorimula* in having longer, more tapered overhanging cusps, and the filamentous tip of the marginals is unique to *Clypeosectus.*

Two species are known from eastern Pacific hydrothermal vents: the type species, *Clypeosectus delectus,* from the Galapagos Rift and the East Pacific Rise at 13°N and 21°N, and *C. curvus,* known only from the Juan de Fuca Ridge. The two species are distinguished by differences in outline (elongate in *C. delectus,* oval in *C. curvus*), elevation (low in *C. delectus,* high in *C. curvus*), and position of apex (posteriormost in *C. curvus*).

**ETYMOLOGY.** The generic name is a Latin

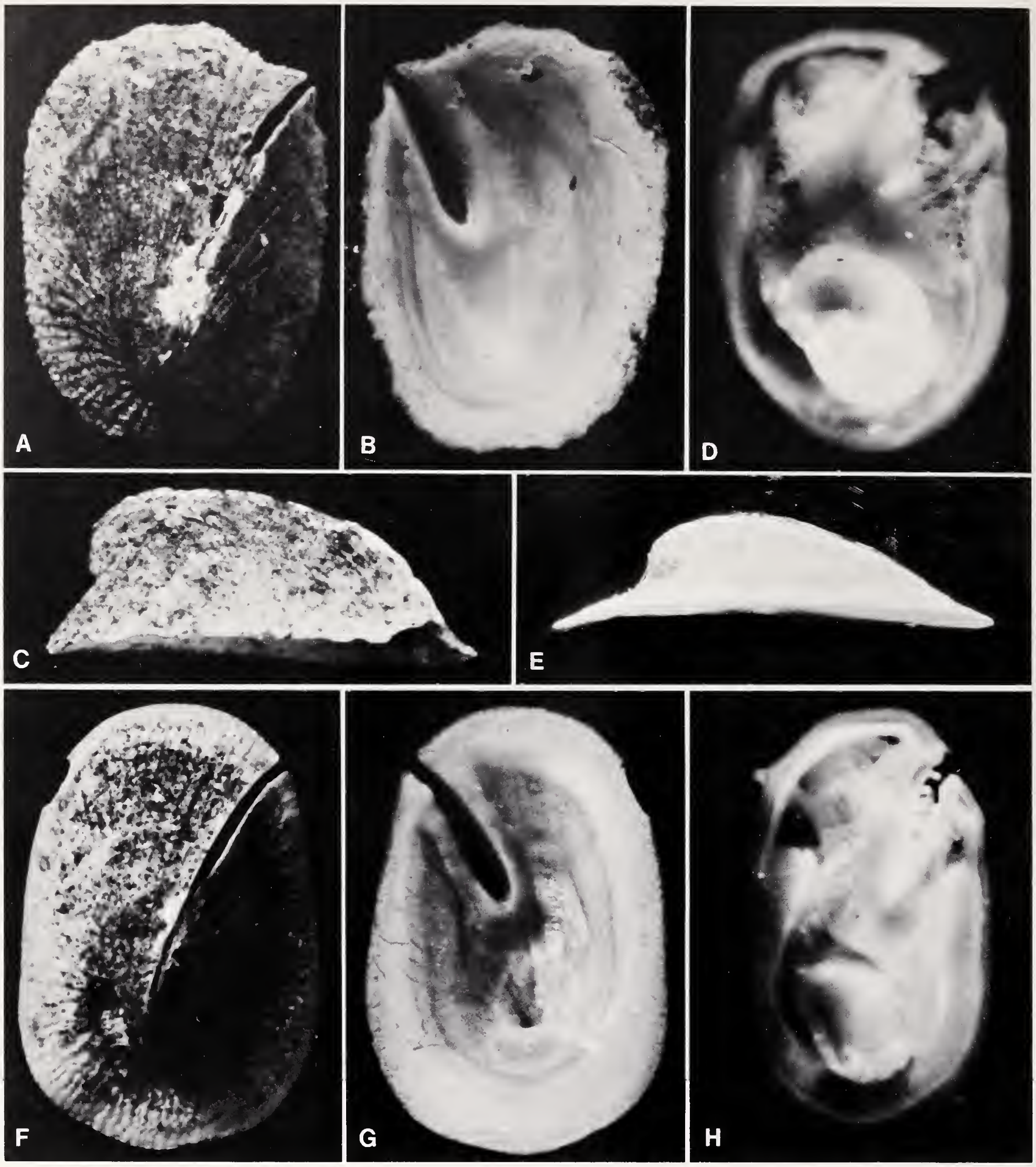

**Figure 8.** *Clypeosectus delectus,* shell and external anatomy of specimens from East Pacific Rise. Anterior at top in dorsal and ventral views. **A–D.** MNHN, uncatalogued, shell margin decalcified and broken back. East Pacific Rise at 13°N, *Cyana* dive 82-36. Length 3.2 mm. **A.** Shell exterior, showing scattered black mineral deposits. **B.** Interior, showing extended muscle scar produced by pallial attachment scar. **C.** Right side. **D.** Detached body, dorsal view, showing bipectinate ctenidia. **E–H.** LACM 2361a. East Pacific Rise at 21°N, *Alvin* dive 1221. Length 3.9 mm. **E.** Right side. **F.** Exterior view. **G.** Interior view. **H.** Detached body, dorsal view, showing bipectinate ctenidia.

compound of *clypeus,* shield, and *sectus,* cut. Gender: masculine.

## *Clypeosectus delectus* new species

Figures 7A–H, 8A–H, 9A–F, 11A–E

Unnamed slit-limpet; Turner, 1980, fig. 1; Hickman, 1983:75, fig. 5 [radula]; Lutz, Jablonski, and Turner, 1984, fig. 1a; Turner, Lutz, and Jabloski, 1985, figs. 9a,b [juvenile shell and protoconch from Galapagos Rift], figs. 10a–c [juvenile shell and protoconch from East Pacific Rise at 21°N].

**DIAGNOSIS.** Outline elongate, profile low, sculpture of narrow radial ribs, apex at three-fourths shell length from anterior margin.

**DESCRIPTION.** Shell (Figs. 7A–H, 8A–C,E–G, 9A–F) small, but relatively large for genus, maximum length 5.2 mm, thin; periostracum thin, pale yellow-brown; outline of aperture elongate oval,

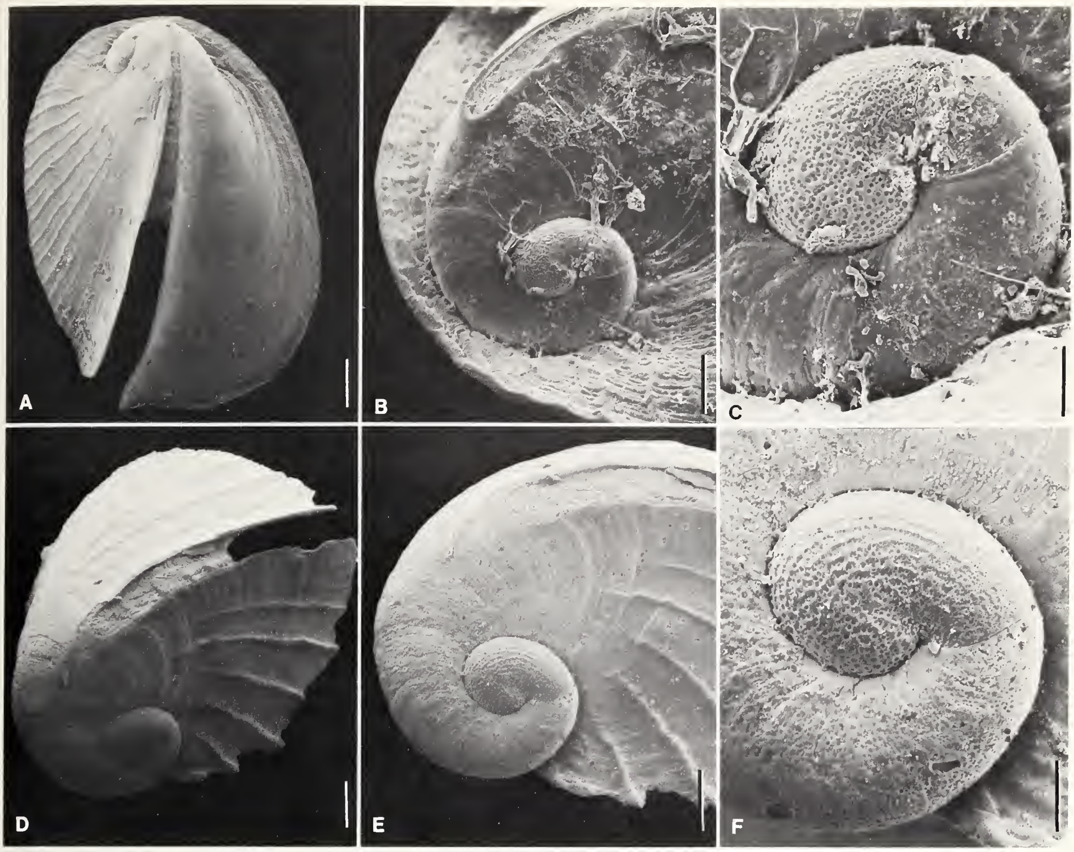

**Figure 9.** *Clypeosectus delectus,* juvenile shells and protoconchs (after Turner et al., 1985, figs. 9, 10). **A–C.** Galapagos Rift, *Alvin* dive unknown. **A.** Dorsal view, anterior at bottom. Scale bar = 200 μm. **B.** Posterior lateral view, showing protoconch and selenizone. Scale bar = 100 μm. **C.** Enlarged view of protoconch, showing ridges and deep pitting. Scale bar = 50 μm. **D–F.** East Pacific Rise at 21°N, *Alvin* dive 1226. **D.** Posterior dorsal view. Scale bar = 100 μm. **E.** Lateral view. Scale bar = 100 μm. **F.** Enlarged view of protoconch, showing ridges and deep pitting. Scale bar = 50 μm.

either end may be broader than the other; margin of aperture in same plane; apical whorl at three-fourths shell length from anterior margin; highest elevation of shell at about half its length. Profile low, height of holotype 0.23 times length. Protoconch diameter 200 μm; protoconch sculpture of fine pitting (Figs. 9C,F); first teleoconch whorl smooth, rounded, not descending below level of protoconch. Slit arising at position of three-fourths whorl in first teleoconch whorl, at which stage aperture expands to produce limpet form through one-half whorl of additional rotation. Slit open one-half shell length in dorsal view, directed to right at angle of approximately 30 degrees off mid-dorsal line. Slit-borders sharply raised, slit open at edge of shell. Selenizone depressed below slit-border; additions to selenizone U-shaped. Sculpture of fine, sharply raised ribs (spiral cords); concentric (axial) sculpture weak, of fine growth lines only. Additional ribs arise in interspaces and assume equal prominence so that pattern of primary and secondary ribs not apparent. Shell edge thin. Muscle scar deeply impressed, continuous anteriorly with broad pallial attachment scar extending almost to slit on both sides (extent of forward position of muscle discernible on preserved specimens). Shell interior transparent at muscle scar, through which exterior sculpture visible; shell interior outside pallial line with frosted surface; slit bordered by heavy deposition of callus along inner side.

**External Anatomy** (Figs. 7D,E,G, 8D,H). As described for genus.

**Internal Anatomy.** Described by Haszprunar (1989).

**Radula** (Figs. 11A–E). As described for genus. Nine pairs of lateral teeth, outermost attached to lateromarginal plate. Marginal teeth with extremely long, filamentous cusps (Figs. 11B,E).

**DIMENSIONS.** Length 5.2, width 3.7, height 1.2 mm (holotype).

**TYPE LOCALITY.** Hydrothermal vents of Galapagos Rift (00°48.0′S, 86°13.0′W), 2451 m.

**TYPE MATERIAL.** Holotype and two paratypes from *Alvin* dive 984, 1 December 1979. Ho-

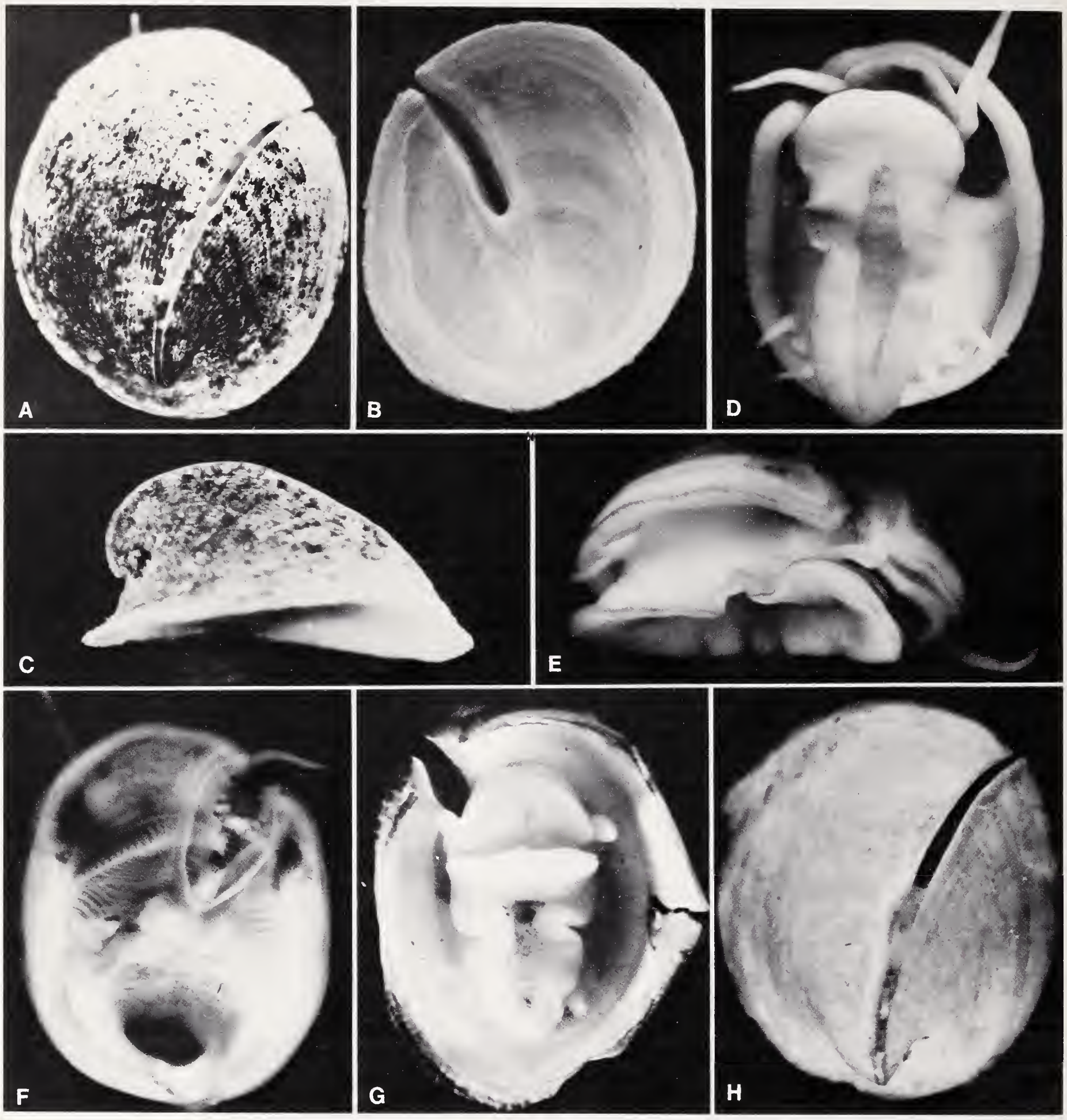

**Figure 10.** *Clypeosectus curvus*, shell and external anatomy. Anterior at top in dorsal and ventral views. **A–C.** USNM 859977, holotype shell. Axial Seamount, Juan de Fuca Ridge, *Pisces IV* dive 1730. Length 4.6 mm. **A.** Exterior, surface encrusted with black mineral deposits. **B.** Interior. **C.** Right side. **D–F.** Body of holotype. **D.** Ventral view, showing three posterior pairs of epipodial tentacles. **E.** Right side. **F.** Dorsal view, showing bipectinate ctenidia and retracted pallial tentacles bordering slit. **G.** LACM 2363, paratype, ventral view with body attached, showing decalcification at margin. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1447. Length 2.4 mm. **H.** LACM 2364a, paratype, exterior view, surface free of mineral deposits. Axial Seamount, Juan de Fuca Ridge, *Pisces IV* dive 1730. Length 4.0 mm.

lotype, USNM 859970 (body sectioned). Paratypes from this and other *Alvin* dives at the Galapagos Rift in 1979 are distributed as specified in Tables 1 and 2.

The holotype (Figs. 7A–C) is the largest and best-preserved specimen from the Galapagos Rift. There are only six specimens of 4.0 mm in length or larger and most are now in damaged or broken condition. Most specimens are decalcified at the margin.

**DISTRIBUTION.** Hydrothermal-vent habitat at Galapagos Rift and at 13°N and 21°N on the East Pacific Rise.

**REMARKS.** This species is the largest of the two members of the genus and has the lowest profile.

Radial sculpture in C. *delectus* is variable in strength. The holotype (Figs. 7A,C) has rather fine sculpture compared to other specimens from the Galapagos Rift (Figs. 7F,H) and the East Pacific Rise

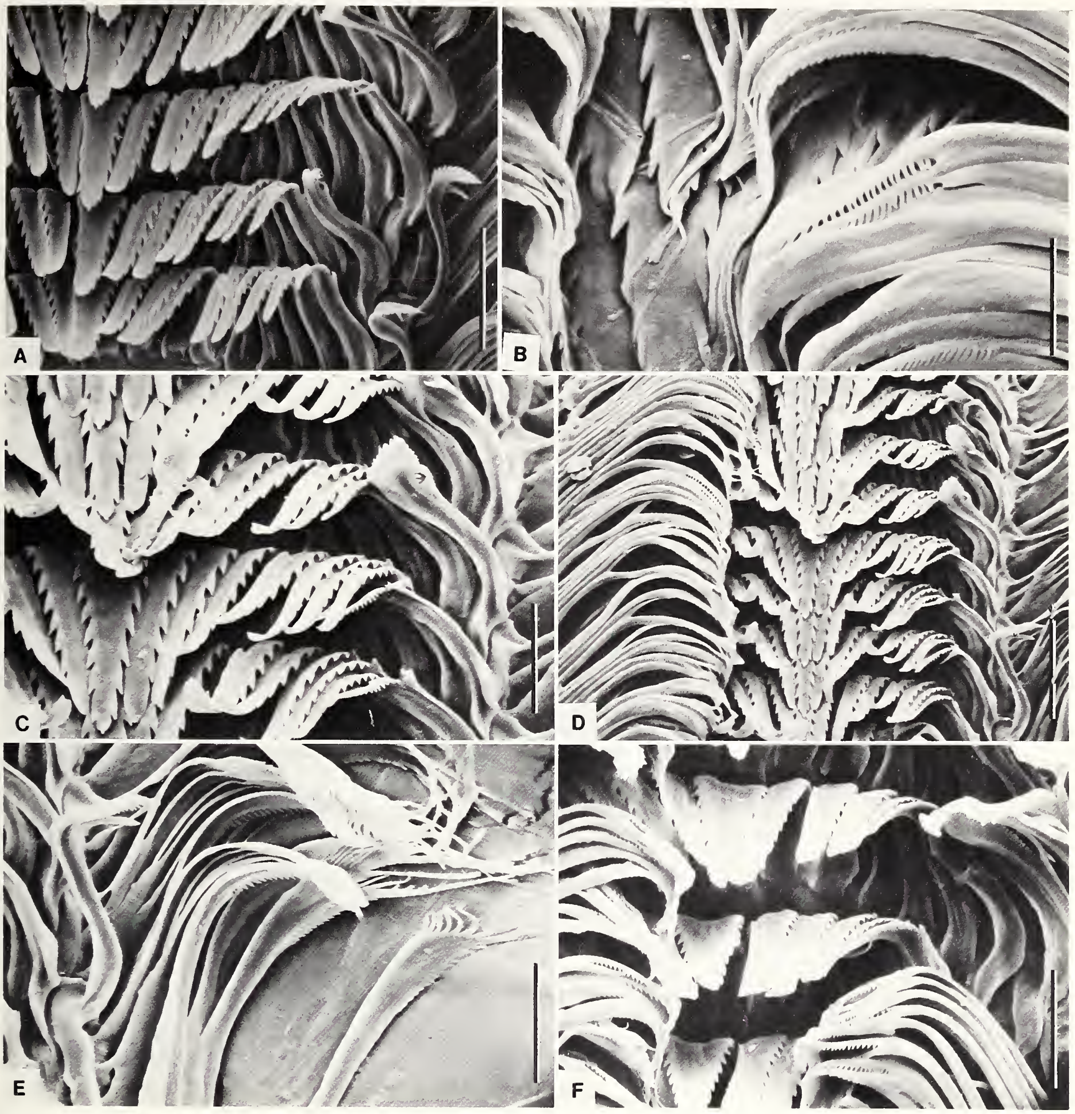

**Figure 11.** SEM views of radulae of *Clypeosectus* species. **A.** *C. delectus,* rachidian and laterals (courtesy C. Hickman). Galapagos Rift, *Alvin* dive 733. Scale bar = 30 μm. **B.** *C. delectus,* showing filamentous tips of marginals folded over central field. LACM 2358. Galapagos Rift, *Alvin* dive 984. Scale bar = 10 μm. **C–E.** *C. delectus.* MNHN. East Pacific Rise at 13°N, *Cyana* dive 83-36. C. Central field, showing rachidian and marginals on right side. Scale bar = 20 μm. **D.** Full width of ribbon, showing marginals of left side folded over and those of right side folded back. Scale bar = 40 μm. **E.** Enlarged view of base of marginals, showing fusion at base and filamentous tips. Scale bar = 20 μm. **F.** *C. curvus,* rachidian laterals and marginals. LACM 2363. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1447. Scale bar = 20 μm.

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at 13°N (Figs. 8A–C) and 21°N (Figs. 8E–F). There is little doubt that a single, highly variable species is represented. Radular characters of specimens from the Galapagos Rift (Fig. 11A) agree with those from 13°N (Figs. 11C–E). Protoconchs of specimens from the Galapagos Rift (Figs. 9A–C) compare well with those from 21°N (Figs. 9D–F).

**ETYMOLOGY.** The name is a Latin adjective meaning delightful.

## *Clypeosectus curvus* new species

Figures 10A–H, 11F

Slit-limpet; Tunnicliffe, 1988:353.

**DIAGNOSIS.** Outline broadly oval, profile high; apex more posterior and sculpture finer than that of *C. delectus.*

**DESCRIPTION.** Shell (Figs. 10A–C,G,H) small, but moderately large for genus, maximum length 4.8 mm; periostracum thin, pale yellow-brown; outline of aperture broadly oval, nearly circular, neither end broader than other; margin of aperture not in same plane, sides raised relative to ends; apical whorl at nine-tenths shell length from anterior margin; highest elevation of shell at about two-thirds shell length from anterior margin. Profile high, height of holotype 0.43 times that of length. Protoconch sculpture unknown (coated on all specimens). First teleoconch whorl rounded, slightly descending below level of protoconch. Slit arising at position of three-fourths whorl in first teleoconch whorl, at which stage aperture expands to produce limpet form through one-half whorl of additional rotation. Slit open nearly half length of shell in dorsal view, directed to right in smooth, even curve, its position at lip at about 40 degrees off mid-dorsal line. Slit-borders sharply raised, slit open at edge of shell. Selenizone depressed below slit-border, additions to selenizone U-shaped. Radial sculpture of fine ribs; ribs arise in interspaces and assume equal prominence with original ribs so that pattern of primary and secondary ribs not apparent. Shell edge thin, easily broken. Muscle scar impressed, continuous anteriorly with broad pallial attachment scar extending anteriorly almost to slit on both sides (extent of forward position of muscle discernible from preserved specimen). Shell interior opaque, tending to be more transparent at muscle scar. Slit bordered by heavy deposition of callus on interior surface.

**External Anatomy** (Figs. 10D–G). As described for genus.

**Internal Anatomy.** Described by Haszprunar (1989).

**Radula** (Fig. 11F). As described for genus. Six pairs of lateral teeth, outermost lateral originating from basal unit regarded as lateromarginal plate; serrations of marginal teeth more numerous and more closely spaced than those of lateral teeth. Marginal teeth with filamentous distal tips.

**DIMENSIONS.** Length 4.6, width 4.0, height 2.0 mm (holotype).

**TYPE LOCALITY.** Hydrothermal vents near summit of Axial Seamount, Juan de Fuca Ridge off Washington (45°59.5′N, 130°03.5′W), 1575 m.

**TYPE MATERIAL.** Holotype and four paratypes from *Pisces IV* dive 1730, 31 July 1986. Holotype, USNM 859976. Additional paratypes from Axial Seamount and from Explorer Ridge near 50°N and Endeavour Segment, Juan de Fuca Ridge (Tables 1, 2). The holotype body remains wet-preserved; two paratype bodies were sectioned. Most of the specimens show some decalcification at the margin, although for the most part the material is in better condition than that of *C. delectus.* No juvenile specimens of *C. curvus* are known; the smallest known specimen has a length of 2.3 mm.

**DISTRIBUTION.** Hydrothermal-vent community of Explorer Ridge (49°45.6′N) and Juan de Fuca Ridge. On the Juan de Fuca Ridge known from Endeavour Segment (47°57.0′N) and Axial Seamount (45°59.5′N) (Table 1).

**REMARKS.** This species differs from *C. delectus* in having an oval, nearly circular outline. The apical whorl is more posterior, the slit is more deflected to the right, the profile is higher, and the radial sculpture is finer than that of *C. delectus.*

**ETYMOLOGY.** The specific name is Latin for curved, calling attention to the curve of the selenizone in dorsal view.

## *Pseudorimula* new genus

**TYPE SPECIES.** *Pseudorimula marianae* new species.

**DESCRIPTION.** Elevation moderate, apex deflected to right, posterior to center, not overhanging posterior margin. Foramen not curving to right in dorsal view; foramen sealed anteriorly. Mature shell nearly symmetrical; sculpture of raised lamellar elements aligned with strong radial ribs. Muscle scar consisting of three nearly equal elements: two lateral and one posterior elements.

**External Anatomy.** Anterior end of foot broad, foot tip with double anterior edge marking opening of anterior pedal gland; foot posterior rounded. Cephalic tentacles relatively long (preserved, contracted condition). Four posterior pairs of epipodial tentacles, on body wall midway between foot edge and thick border of mantle margin; two anterior pairs, with thick, joined bases, each with narrow projecting tips. Mantle skirt deeply emarginate, corresponding to foramen and seam in shell, edge of emargination with projecting papillae. Mantle skirt above head thin, nearly transparent. Shell muscles without hooks, macroscopically separate posteriorly; third muscle present posteriorly. Ctenidia of nearly equal size, right ctenidium slightly smaller.

**Radula.** Radular ribbon nearly symmetrical. Rachidian tooth with long, rounded, overhanging tip, edges serrated; shaft of rachidian broad at base. Five pairs of lateral teeth, similar in morphology to rachidian, outer edges with fine serrations, inner edges smooth; size of overhanging tips decreasing gradually away from rachidian, shafts of laterals increasing in length away from rachidian. Fifth lateral continuous with basal element regarded as lateromarginal plate; enlarged outer lateral lacking. Marginal teeth numerous, with spatulate tips, edges finely and sharply serrated, serrations similar to those of laterals. Marginals and outer laterals with one long denticle on outer edge of shaft near overhanging tip.

**REMARKS.** Unlike *Clypeosectus, Pseudorimula* has the slit sealed anteriorly, producing a shell that is stronger than that of *Clypeosectus,* many shells of which are broken in the present material. In this aspect it is convergent with shell morphology of the fissurellid genus *Rimula* Defrance, 1827, which is a structural improvement over the design of *Emarginula* Lamarck, 1801. The greater symmetry of *Pseudorimula* also trends toward the condition

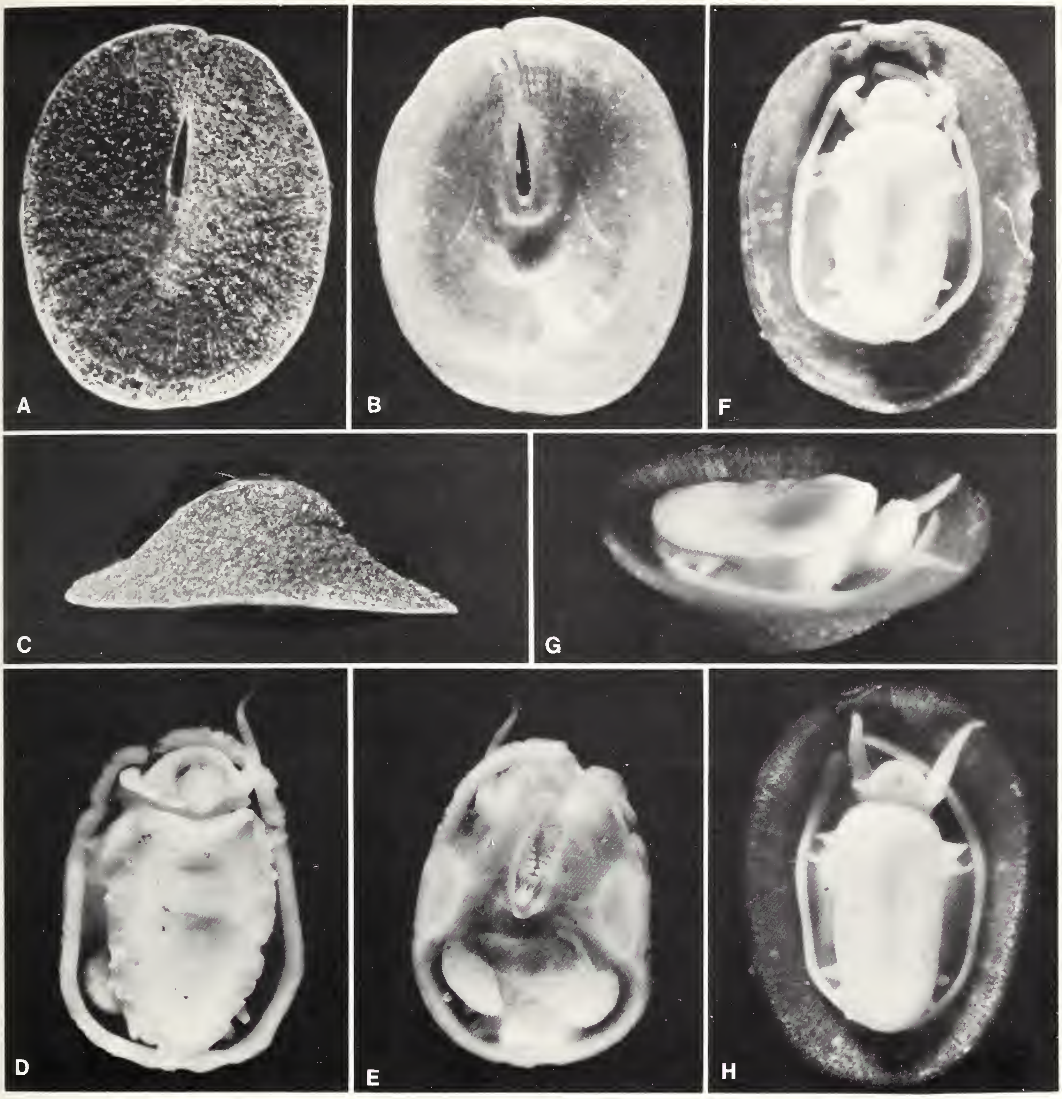

Figure 12. *Pseudorimula marianae,* shells and external anatomy. All from Mariana Back-Arc Basin, *Alvin* dive 1836. Anterior at top in all dorsal and ventral views. **A–C.** USNM 859977, holotype. Length 6.4 mm. **A.** Exterior, with thick coat of black mineral deposits. **B.** Interior. **C.** Left side. **D,E.** Body of holotype prior to sectioning. **D.** Ventral view, specimen with radula projecting. **E.** Dorsal view, showing posterior shell muscle and bipectinate ctenidia. **F.** LACM 2366a, paratype with body attached, ventral view. Length 6.1 mm. **G,H.** LACM 1366b, immature paratype specimen with body attached. Length 4.2 mm. **G.** Right side. **H.** Ventral view.

of nearly complete symmetry of fissurellids. The sculpture of *Pseudorimula* is also more characteristic of fissurellids in having primary and secondary ribs that increase in prominence with growth.

The muscle configuration, in which there is an irregular posterior element, is highly unusual, and is unknown in other limpet families. *Pseudorimula* has more pairs of epipodial tentacles than does *Clypeosectus,* thereby approaching the fissurellid condition to a greater extent than the latter genus. *Pseudorimula* further differs in lacking the genital process of *Clypeosectus.*

Only a single radular preparation for the type species was possible. As in *Clypeosectus,* there is difficulty in distinguishing between lateral and marginal teeth, which have similar morphology. The radula is very similar to that of *Clypeosectus,* including the presence of the long denticle on the outer edge of the shaft of the outer laterals and marginals, and the tendency of laterals and marginals to have a similar appearance. There is, however, no indication of the filamentous tip that is characteristic of the marginals of *Clypeosectus.* The radula further differs from that of *Clypeosectus* in

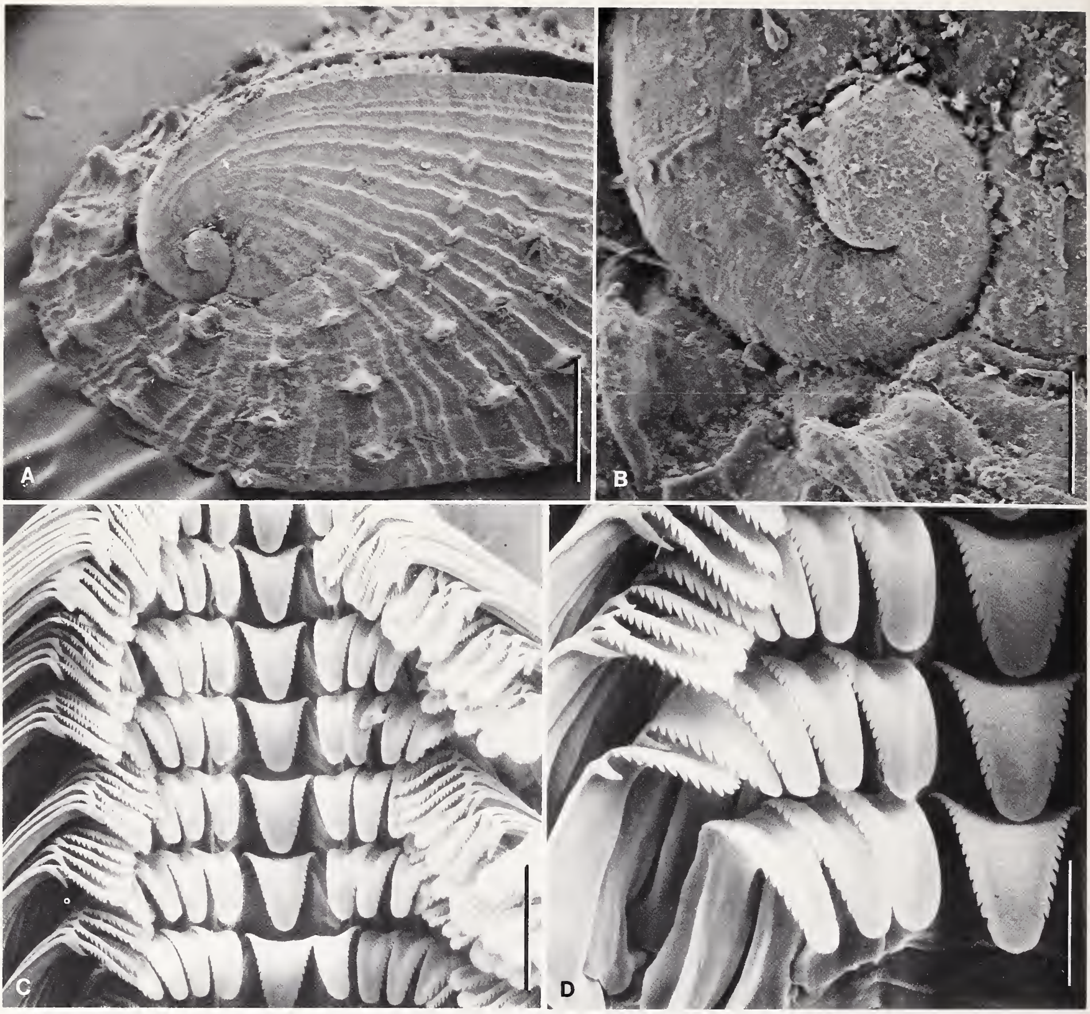

**Figure 13.** *Pseudorimula marianae,* juvenile shell, protoconch and radula. All from Mariana Back-Arc Basin, *Alvin* dive 1836. **A,B.** LACM 2367, immature shell. **A.** Oblique posterior-lateral view of apical area. Scale bar = 400 $\mu$m. **B.** Protoconch. Scale bar = 100 $\mu$m. **C,D.** USNM 859977, radular ribbon from holotype. **C.** Rachidian, laterals, and marginals. Scale bar = 40 $\mu$m. **D.** Enlarged view of rachidian and laterals. Scale bar = 20 $\mu$m.

having a less elongate shaft to the rachidian, a broader cusp with a more rounded tip, the laterals being serrate on the outer edges only, and fewer lateral teeth. There are at least five pairs of lateral teeth in *Pseudorimula marianae,* compared to nine in *C. delectus* and six in *C. curvus.*

*Pseudorimula* is monotypic for *P. marianae,* from the Mariana Back-Arc vents, western Pacific.

**ETYMOLOGY.** The generic name means false *Rimula,* owing to its resemblance to the fissurellid genus *Rimula* Defrance, 1827. Gender: feminine.

### *Pseudorimula marianae* new species

Figures 12A–H, 13A–D

**DIAGNOSIS.** Outline oval, height moderate, sculpture radial with sharp imbrications, apex at two-thirds shell length from anterior margin, foramen one-half length of anterior slope, directed toward right.

**DESCRIPTION.** Shell (Figs. 12A–C,F–H, 13A,B) relatively large for family, maximum length 8.7 mm. Periostracum yellowish brown, tightly adhering, projecting slightly past shell margin and enveloping edge. Outline of aperture oval, slightly broader anteriorly; margin of aperture not in same plane, sides raised relative to ends; highest elevation of shell at about one-half its length. Profile moderately high, height of holotype 0.37 times length. Apical whorl at two-thirds shell length from anterior end, deflected to right; protoconch length 200 $\mu$m, surface finely reticulate (Fig. 13B), first teleoconch whorl smooth, rounded, slightly descending below level of protoconch; slit arising three protoconch diameters away at position of one-half whorl of growth in first teleoconch whorl, at which stage expansion of aperture produces limpet form through one-half whorl of additional rotation. Slit open one-half length of anterior slope, slightly deflected to right. Borders of foramen slightly raised, except anteriorly, where slit sealed and its trace slightly depressed. Selenizone weakly depressed below slit-border, additions to selenizone extending straight across. Sculpture of about 22 sharply defined primary ribs with one to three secondary ribs of equal prominence arising in interspaces. Concentric sculpture of fine growth lines, raised into sharp lamellar scales on crossing primary ribs. Muscle scars three, anterior-lateral scars rounded anteriorly, not joined to form horseshoe-shaped posterior element, but represented posteriorly by large irregular muscle scar. Anterior pallial attachment scars faint. Position of muscles more readily determined from comparison with preserved specimens. Thick seam of interior callus strengthens shell anterior to slit; interior further strengthened by transverse callus posterior to apical pit. Shell interior somewhat transparent, especially in region of muscle scars.

**External Anatomy** (Figs. 12D–H). As described for genus.

**Internal Anatomy.** Described by Haszprunar (1989).

**Radula** (Figs. 13C,D). As described for genus, with at least five pairs of lateral teeth.

**DIMENSIONS.** Length 6.4, width 5.2, height 2.4 mm (holotype).

**TYPE LOCALITY.** Snail Pit vents, Mariana Back-Arc Basin (18°10.95′N, 144°43.2′E), 3660 m.

**TYPE MATERIAL.** Holotype and three paratypes from *Alvin* dive 1836, 27 April 1987. Holotype USNM 859977. The holotype had the radula protruding, from which a piece was removed for the SEM preparation. One additional paratype (smallest specimen) from Alice Springs vent, Mariana Back-Arc Basin, *Alvin* dive 1843, 4 May 1987. For measurements and disposition of paratypes see Tables 1 and 2.

The three largest specimens are coated with black mineral deposits that partially obscure the sculpture. The two smallest specimens are relatively free of encrustations and show the periostracum.

**REMARKS.** The smallest shell (Figs. 13A,B) (length 2.7 mm) has a relatively longer foramen than that of the larger specimens, indicating that the foramen does not enlarge proportionally with increase in shell length.

**ETYMOLOGY.** The name refers to the type locality.

## DISCUSSION

Haszprunar shows in Part 2 (1989) that the slit-limpets represent two different anatomical plans that differ at the superfamily level, but which may be accommodated within existing superfamilies, the Scissurellacea (separated from Pleurotomariacea by Haszprunar) and the Fissurellacea. One group, the Clypeosectidae, differs sufficiently, particularly in its reproductive anatomy, to warrant the establishment of a new family within the Fissurellacea. In the Scissurellacea, however, there are not sufficient differences in the internal anatomy to warrant the establishment of a separate family for the hydrothermal-vent genera, although there are radular and protoconch differences, as well as differences in anatomical details that justify the erection of two new subfamilies for these genera. Here I discuss the shell and radular characters that support the recognition of new suprageneric taxa in both superfamilies.

## CHARACTER STATES

### Protoconch

Sculpture of strong collabral ridges on the protoconch of *Scissurella, Sinezona* (Fig. 6C), and *Incisura* (Fig. 6E) is an apomorphy within Scissurellidae, limited to the most derived subfamily Scissurellinae. Lack of such sculpture in both the Temnocinclinae and the Clypeosectidae is clearly primitive, as it is unknown elsewhere among fossil and Recent archaeogastropods.

The finely ridged and deeply pitted protoconch of *Sutilizona* (Figs. 4D–F) is comparable to that of *Clypeosectus* (Figs. 9A–F). This evidently represents convergence between unrelated genera in different superfamilies.

### Teleoconch Sculpture

All previously known scissurellids other than *Incisura* (Fig. 6B) have strong axial (collabral) elements on the early teleoconch, a trait that is also shared with the new genera in the Temnocinclinae and Sutilizoninae (Figs. 4A–F). In contrast, fissurellids have strong spiral sculpture on the early teleoconch, never showing strong collabral sculpture at this stage of growth. The early sculpture of *Clypeosectus* (Figs. 9A–F) and *Pseudorimula* (Figs. 13A,B) is spiral, and comparable to that of fissurellids, except that the transition to the first teleoconch whorl does not include a sudden increase in diameter, as is frequent for fissurellids (e.g., McLean, 1985, fig. 7B).

In fissurellids the basic pattern of sculpture consists of primary radial (spiral) ribs that increase in size with growth, between which secondary and tertiary ribs appear and remain discernible. In *Anatoma* the secondary spiral cords attain the strength of the primary cords and become indistinguishable so that sculptural elements increase in number, not size. This is true also of *Temnocinclis*. However, *Temnozaga* has primary and secondary ribs that remain distinct, which implies a closer affinity of the latter genus to the Fissurellidae, but is more likely due to convergence.

The punctations that form pits on the early teleoconch sculpture of fissurellids are not present in any scissurellid or in the clypeosectids. Herbert and Kilburn (1986:1, figs. 1–6) showed that processes of the mantle penetrate through pores in the shell and reach the exterior pits in fissurellids. Bandel (1982) suggested these processes to be homologous with aesthetes of chitons. If so, it would be an ancestral, plesiomorphic character. However, the polarity of this character is not clear, as it is limited to only a single archaeogastropod family.

### Slit

The slit in fissurellids may start early, almost in contact with the protoconch lip (e.g., *Nesta candida* H. Adams, 1870, figured by Bandel, 1982, pl. 10, fig. 3, and *Puncturella voraginosa* Herbert and Kilburn, 1986, fig. 68), or, more commonly, it may arise at one or more protoconch diameters away (e.g., *P. capensis* Thiele, 1919, figured by Herbert and Kilburn, 1986, fig. 65). In all scissurellids and in clypeosectids it starts three-fourths to one whorl away from the protoconch lip. An early start in some fissurellids is likely a convergent, derived character.

A sharply raised border to the slit and a depressed selenizone is a trait of all scissurellids and clypeosectids, but not of such fissurellid genera as *Emarginula* and *Rimula.* In the Fissurellacea this character is diagnostic for clypeosectids.

Among zeugobranchs, an open slit is primitive, whereas a closed slit is a convergent, derived character. Polarity in this character is evident from study of the fossil record of many zeugobranchs. Most groups, including three of the scissurellid subfamilies, as well as the clypeosectids and fissurellids, have representative genera with both conditions. The closed slit imparts obvious mechanical strength to the shell.

### Shell Muscle Scars

Emarginuline fissurellids (the oldest and most primitive members of the family) have unique hook-shaped terminations to the muscles and scars (e.g., MacClintock, 1963; McLean, 1984). The genera of the youngest fissurellid subfamily (Fissurellinae) and the two genera of clypeosectids lack the hooks. The apparent hook-shaped process of the left muscle scar of *Clypeosectus delectus* in Figure 7B is actually made by an extension of the pallial attachment muscle. Absence of hooks is a diagnostic, apomorphic character for Clypeosectidae.

Among scissurellids, the shell muscle of *Incisura* lacks hooks and is not joined posteriorly. *Temnocinclis* and *Temnozaga* are the first known scissurellid limpets with horseshoe-shaped muscles. Hook-shaped muscles are unknown in scissurellids.

The unusual shell muscle configuration of *Pseudorimula,* in which there are two lateral muscles and a single posterior muscle, is unlike that of all other limpets among diverse families. It is surprising that only one of the two clypeosectid genera has this condition. The evolutionary advantage of this tripartite pattern is unknown. Systematists who base their classifications on shell muscle conditions should take note of this apparently unique case.

### Radular Morphology

In the Scissurellidae, the temnocincline radula and the sutilizonine radula differ from those of anatomine and scissurelline scissurellids in lacking the enlarged fourth lateral that heretofore had been considered a hallmark of the family. There is a similar comparison within the Fissurellacea. The presence of an enlarged tooth is a hallmark of the Fissurellidae. Although clypeosectids are unique in having a relatively large number of lateral teeth (5 to 9 pairs), the chief distinctive feature of the clypeosectid radula is the lack of an enlarged outer lateral tooth. Thus, temnocinclines, sutilizonines, and clypeosectids are comparable in lacking enlarged outer laterals.

Character polarity for the lack of an enlarged lateral in the hydrothermal-vent slit-limpets is not clear. Lack of such a tooth could be primitive in both superfamilies or, more likely, it may represent a convergent loss, possibly due to less need for feeding specialization in the hydrothermal-vent habitat. Feeding by browsing on the bacterial films that are ubiquitous in the hydrothermal-vent habitat may not require the strongly developed outer lateral teeth. In fissurellids, the enlarged outer lateral teeth are the most functional, working teeth. However, food sources in shallow-water environments are more diverse and tougher in composition, including sponges, the principal food of emarginuline fissurellids.

Asymmetry in the rhipidoglossate radula has been discussed by Hickman (1981, 1983, 1984a). Asymmetry is unknown in scissurellid radulae, whereas most fissurellids have a moderately to highly asymmetrical radula. In fissurellids the asymmetry is correlated with the greatly enlarged fifth lateral and the necessity to stagger the placement of this element when the ribbon is folded. Although the anatomine and scissurelline scissurellids have an enlarged fourth lateral, it is not sufficiently large to require staggering of the opposing elements when this ribbon is enrolled; consequently, the scissurellid radula remains symmetrical. The clypeosectid radula is also symmetrical at least partly due to the lack of an enlarged outermost lateral tooth.

## FOSSIL RECORD OF SCISSURELLIDAE

Although the first appearance of Scissurellidae is cited as Cretaceous (Knight et al., 1960), K. Bandel (pers. comm. to G. Haszprunar) reports a Triassic record of the family.

Batten (1975) and Bourne (1910) argued that scissurellids were neotenously derived from fissurellids, basing their arguments in large part on the depiction by Boutan (1885, pl. 42, fig. 5) of a scissurellid juvenile purported to represent a stage in fissurellid development. The supposed "*Scissurella*-stage" in fissurellid ontogeny was based on a misidentification of that figure, as separately noted by both Bandel (1982) and further detailed by McLean (1984, caption to fig. 6).

## FOSSIL RECORD OF FISSURELLIDAE

The Fissurellidae are traceable to the Middle Triassic and underwent a substantial radiation in the Jurassic (Knight et al., 1960; McLean, 1984).

Earlier (McLean, 1984) I presented arguments in support of the scenario that fissurellids were derived from Paleozoic bellerophontaceans, developing an idea proposed originally by Golikov and Starobogatov (1975). No further evidence in support of this theory has been offered. Two primary objections remain: there is asymmetry in the ontogeny of all fissurellids, and the punctations or pores in the early teleoconch of fissurellids have not been detected in bellerophontaceans. As noted most recently by Hickman (1988), the question of bellerophontacean affinities remains as controversial as ever.

## TIME OF ENTRY TO THE HYDROTHERMAL-VENT COMMUNITY

Earlier (McLean, 1985, 1988a, 1988b, 1989), I hypothesized that the newly described families and superfamilies of archaeogastropod limpets (Neomphalacea, Lepetodrilacea, Peltospiracea) from the hydrothermal-vent community entered this community by the early Mesozoic, the time of divergence and origin of other living archaeogastropod superfamilies, and a time in which archaeogastropods were the dominant gastropods in shallow seas. Fissurellaceans and scissurellaceans had an early Mesozoic origin and there is no reason to disallow a Mesozoic origin for temnocincline and sutilizonine scissurellids and the clypeosectid fissurellaceans. The argument, however, is less compelling than for the other newly described superfamilies because the rank of endemism (see Newman, 1985), i.e., the hierarchical level of new taxa, is below the superfamily level for the slit-limpets.

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# CONTRIBUTIONS IN SCIENCE

## NEW SLIT-LIMPETS (SCISSURELLACEA AND FISSURELLACEA) FROM HYDROTHERMAL VENTS. PART 2. ANATOMY AND RELATIONSHIPS

GERHARD HASZPRUNAR

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# NEW SLIT-LIMPETS (SCISSURELLACEA AND FISSURELLACEA) FROM HYDROTHERMAL VENTS. PART 2. ANATOMY AND RELATIONSHIPS

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GERHARD HASZPRUNAR[1]

**ABSTRACT.** The anatomy of the slit-limpets from the deep-sea hydrothermal-vent communities belonging to the Scissurellidae and Fissurellacea, which are described by McLean (1989b), is presented.

*Temnocinclis euripes* and *Temnozaga parilis* have scissurellid anatomy, but differ from other scissurellids in sharing largely symmetrical shells, equally shaped and structured monopectinate ctenidia, smooth cephalic and epipodial tentacles, diagnostic radular features and statocysts, and in lacking eyes. Both are therefore united in the subfamily Temnocinclinae. *Sutilizona theca* also has scissurellid anatomy, differing from other scissurellids in having diagnostic protoconch sculpture, a peculiar gland at the anterior left pallial roof, monopectinate ctenidia, unusually large gonads, diagnostic radular features, a single pair of radular cartilages only, and vestigial eyes.

*Clypeosectus delectus, C. curvus,* and *Pseudorimula marianae* exhibit fissurellacean characters (vestigial left kidney, gonoduct opening in right renopericardial duct, anal gland). In contrast to the fissurellid condition they are characterized by an asymmetrical shell and mantle cavity, lack of shell-muscle hooks, a diagnostic type of epipodium, diagnostic radula, and by lack of a radular caecum and of eyes. In addition, males are equipped with a prostate and a copulatory organ, and females with a receptaculum seminis, both indicating internal fertilization. Based on all of these characters, the species are united in a separate family Clypeosectidae in the Fissurellacea.

The reproductive features of the new groups are briefly discussed and compared with other members of the respective superfamilies. The Pleurotomariacea are regarded as a grade and are split into Scissurellacea, Haliotacea, and Pleurotomariacea *sensu stricto;* the latter are most closely related to the Trochacea.

## INTRODUCTION

Although the close relationship between Pleurotomariidae and Trochidae has been recognized for nearly a century (*e.g.*, Pelseneer, 1899; Bourne, 1910), authors usually have united the Pleurotomariacea and Fissurellacea within the "Zeugobranchia." This was based mainly on the presence of paired ctenidia, the common retention of the shell slit or hole, and on the "*Scissurella*-stage" in fissurellid ontogeny. The latter argument, however, is no longer valid (see McLean, 1989b). The paired ctenidia mentioned above represent a common primitive character, not directly relevant for tracing the relationships of the included groups.

Moreover, until recently, anatomical comparisons between the Scissurellidae and Fissurellidae (Pelseneer, 1899; Bourne, 1910; Fretter and Graham, 1962, 1976) have revealed little affinity between the two families. Scissurellidae have been considered to be part of the evolutionary sequence trending from Pleurotomariacea to Trochacea, in which the foot has a double anterior edge marking the opening of the anterior pedal gland, an asymmetrical mantle cavity, and a well-developed left kidney, a papillary sac. In contrast, adult Fissurellidae never have the foot with a pedal gland, and the left kidney is reduced.

Salvini-Plawen (1980) proposed the suborder "Vetigastropoda" to include the Fissurellacea, Pleurotomariacea, Trochacea, and (tentatively) the Cocculinacea. The last superfamily has more recently been treated as another suborder, the Cocculiniformia (Haszprunar, 1988b). Salvini-Plawen and Haszprunar (1987) have redefined the Vetigastropoda as a clade, restricting the taxon to Fissurellacea, Pleurotomariacea (*sensu lato*), and Trochacea. In contrast to Hickman (1988), who favored a restricted use of "Archaeogastropoda" replacing Vetigastropoda, I still use *Archaeogastropoda* (a grade) and Vetigastropoda (a clade including also the Lepetodrilacea; see Haszprunar, 1988a).

The slit-limpets described here exhibit new combinations of characters among the Vetigastropoda. This necessitates a general reconsideration of the interrelationships of the vetigastropod subgroups. Also the aberrant limpet genus *Neomphalus* (McLean, 1981; Fretter et al., 1981) and the recently described superfamily Lepetodrilacea (McLean, 1988; Fretter, 1988) are to be reconsidered with respect to their vetigastropod affinities. However, in the light of rapid increase of knowledge by means of EM-studies (*e.g.*, Healy, 1988) and several papers

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[1] Institut für Zoologie der Universität Innsbruck, Technikerstraße 25, A-6020 Innsbruck, Austria.

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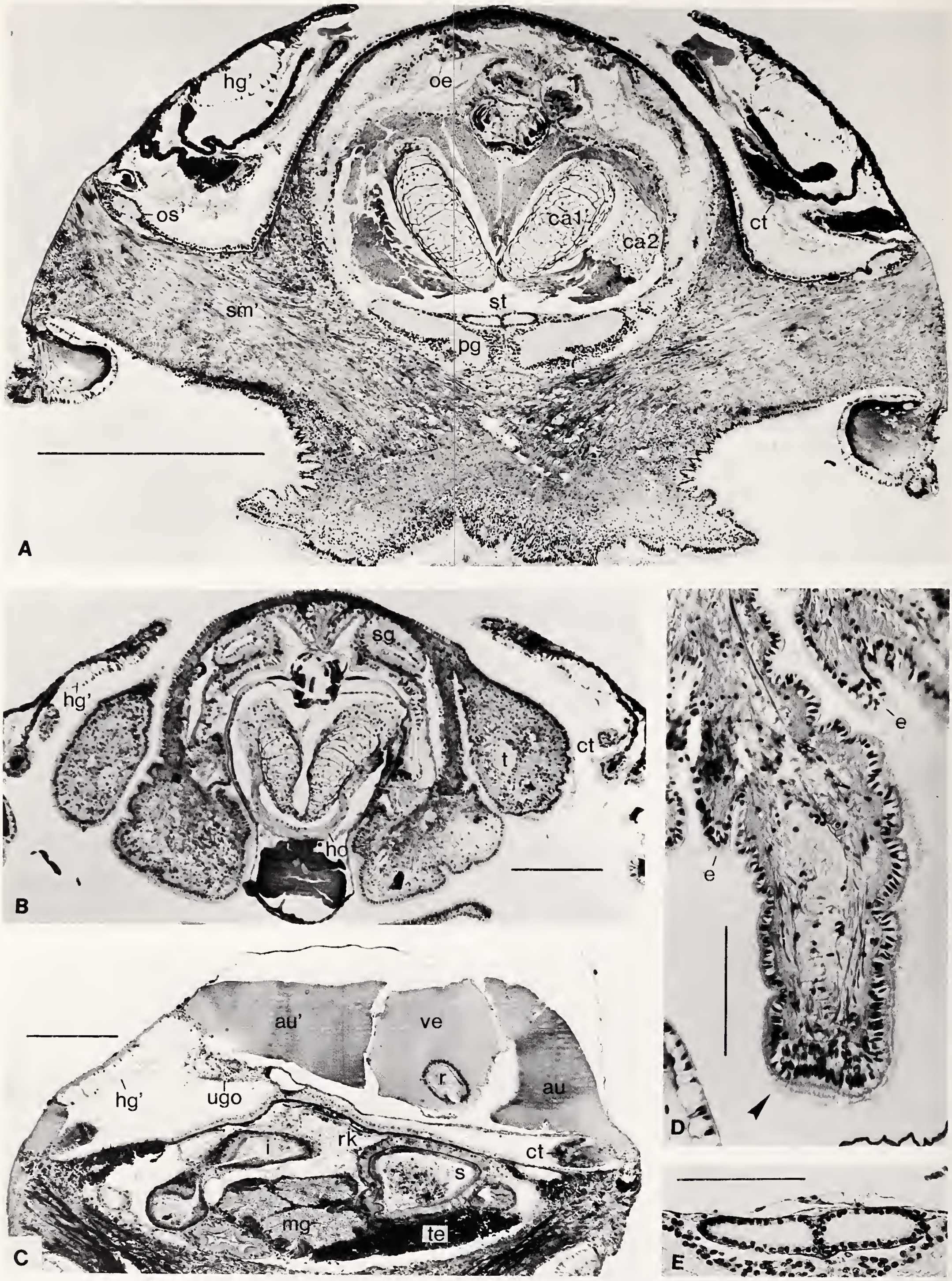

**Figure 1.** *Temnocinclis euripes,* sections of holotype (USNM 859964), all frontal view. **A.** At line of statocysts. Scale bar = 500 μm. **B.** At mouth opening. Scale bar = 200 μm. **C.** At heart. Scale bar = 200 μm. **D.** Epipodium (arrow marks ESO). Scale bar = 100 μm. **E.** Statocysts with tiny statocones embedded in matrix. Scale bar = 100 μm.

Lettering: au, auricle; ca1,2, radular cartilages (anterior, posterior); ct, ctenidium; e, epopodial tentacle; i, intestine; hg, hypobranchial gland; ho, horizontal muscle; mg, midgut gland; oe, oesophagus; os, osphradial ganglion; pc, pericardium; pg, pedal ganglion; r, rectum; rk, right kidney; s, stomach; sg, salivary gland; sm, shell muscle; st, statocysts; t, tentacular nerve; te, testis; ugo, urinogenital opening; ve, ventricle.

describing possibly related forms (McLean, 1989a; Warén and Bouchet, 1989), I restrict this paper to anatomical descriptions, discussion of relationships of genera and families, and of their mode of reproduction. A more general analysis of the phylogeny of the Vetigastropoda is given elsewhere (Haszprunar, 1988a, and in prep.).

## MATERIAL AND METHODS

The specimens investigated anatomically are listed by McLean (1989b: table 2). The preservation of specimens was good, and the anatomy could be reconstructed with sufficient certainty despite the low number of specimens investigated.

Histological section series were prepared at the Universities of Vienna and Innsbruck (see Acknowledgments). Specimens of *Sutilizona theca* were embedded in araldit, serially sectioned at 2 μm, and stained with Redaud's fluid. Specimens of all other species were embedded in paraplast, serially sectioned at 5–10 μm, and stained with azan (Heidenhain's method).

Anatomy of the scissurellid species will be treated further by Marietta Strassoldo (University of Vienna), who has a comparative study on the anatomy and ontogeny of the family Scissurellidae in preparation.

## SCISSURELLACEA—SCISSURELLIDAE

### DIAGNOSIS

(see also McLean [1989b]
and Discussion)

Coiled or limpet-like Vetigastropoda, shell with shell slit or foramen, interior nacre lacking, protoconch of variable sculpture. Two shell muscles lacking hooks. Operculum retained in adults of all genera. Two bi- or monopectinate ctenidia, often of unequal shape and position. Left kidney as papillary sac, the larger right kidney ramifying between viscera, with an urinogenital opening. Never with organs for internal fertilization. Eye-vesicles (if present) closed. Several pairs of epipodial and single pair of separated epipodial sense organs (ESO-)tentacles or several ESO-tentacles alone. Diagnostic radula features (see McLean, 1989b).

### ANATOMY OF *TEMNOCINCLIS EURIPES* AND *TEMNOZAGA PARILIS*

Both species are very similar in anatomy; therefore, a common description is given. Differences between species are mentioned where they occur.

The pedal sole is totally ciliated, and a large pedal gland is present. The mantle border is smooth and contains large blood-sinuses. The monopectinate ctenidia have no free axis, both are of equal length. Only a single skeletal rod is present in the axis, whereas the skeletal elements are paired in the leaflets. The latter are provided with bursicles. The right hypobranchial gland (Fig. 1C: hg′) is much larger than the left, which is limited in its extent by the heart.

The heart is situated somewhat to the left (Fig. 1C) and is functionally diotocardian, the pericardium is large and the auricles are of equal size but not of equal shape (as in *Clypeosectus,* see Figs. 1C, 3: au, au′).

The left kidney is a papillary sac and is smaller than the right one. The right kidney forms a large coelomic system and is fused with the vas deferens (or oviduct, respectively) near their common opening. The species are gonochoristic. In both sexes the gonad occupies the entire left side of the body and posteriorly surrounds the stomach. The sperm cells have very short flagellae or even lack flagellae, thus the appearance of the testis is "granular" (as in *Pseudorimula*). The proximal vas deferens contains a dense mass of ripe sperm cells and obviously has the function of a vesicula seminalis. In the female of *Temnocinclis euripes* (a female of *Temnozaga parilis* has not been investigated anatomically) the ovary contains large yolk-rich eggs, the oviduct is ciliated and non-glandular.

The jaws are massive, the salivary glands are simple and pouchlike (Fig. 1B: sg). There are two radular cartilages (Fig. 1A: ca1, ca2) and the radular sheath is long, making two loops. Compared with the Clypeosectidae the anterior oesophagus lacks a specialized ventral tract and does not encircle the radular sheath. The oesophagus pouches are rather small. In *Temnocinclis euripes* they lack papillae, whereas in *Temnozaga parilis* they are papillate (as in *Clypeosectus,* see Fig. 4D). The posterior oesophagus enters the stomach between the two openings of the midgut glands (as in *Clypeosectus,* see Fig. 5C). The stomach is provided with a gastric shield and protostyle, the caecum is small. The intestine makes several loops, having a distinct groove (as in *Clypeosectus,* see Fig. 5A). The stomach and the intestine contain detritus. The ventricle encircles the rectum, and in contrast to the Clypeosectidae (see below) an anal gland is generally lacking.

The anterior nervous system is hypoathroid in forming a pleuropedal complex. The labial lobes of the cerebral ganglia are large, but no labial commissure could be detected. The visceral loop is streptoneurous with distinct visceral ganglia. Eyes and optical nerves are completely lacking. In *Temnocinclis euripes* the epipodial tentacles are of different types, the second one bears an epipodial sense organ (Fig. 1D). *Temnozaga parilis,* in contrast, has uniform epipodial tentacles, each of which is provided with an epipodial sense organ. In contrast to other vetigastropods a subradular organ is lacking in both genera. The statocysts contain many statocones, each of which is embedded in a small vacuole (Fig. 1E).

### ANATOMY OF *SUTILIZONA THECA*

The mantle slit is to the right, oblique, and is provided with a single tentacle. The mantle cavity is asymmetrical, and deeper at the right side. The two

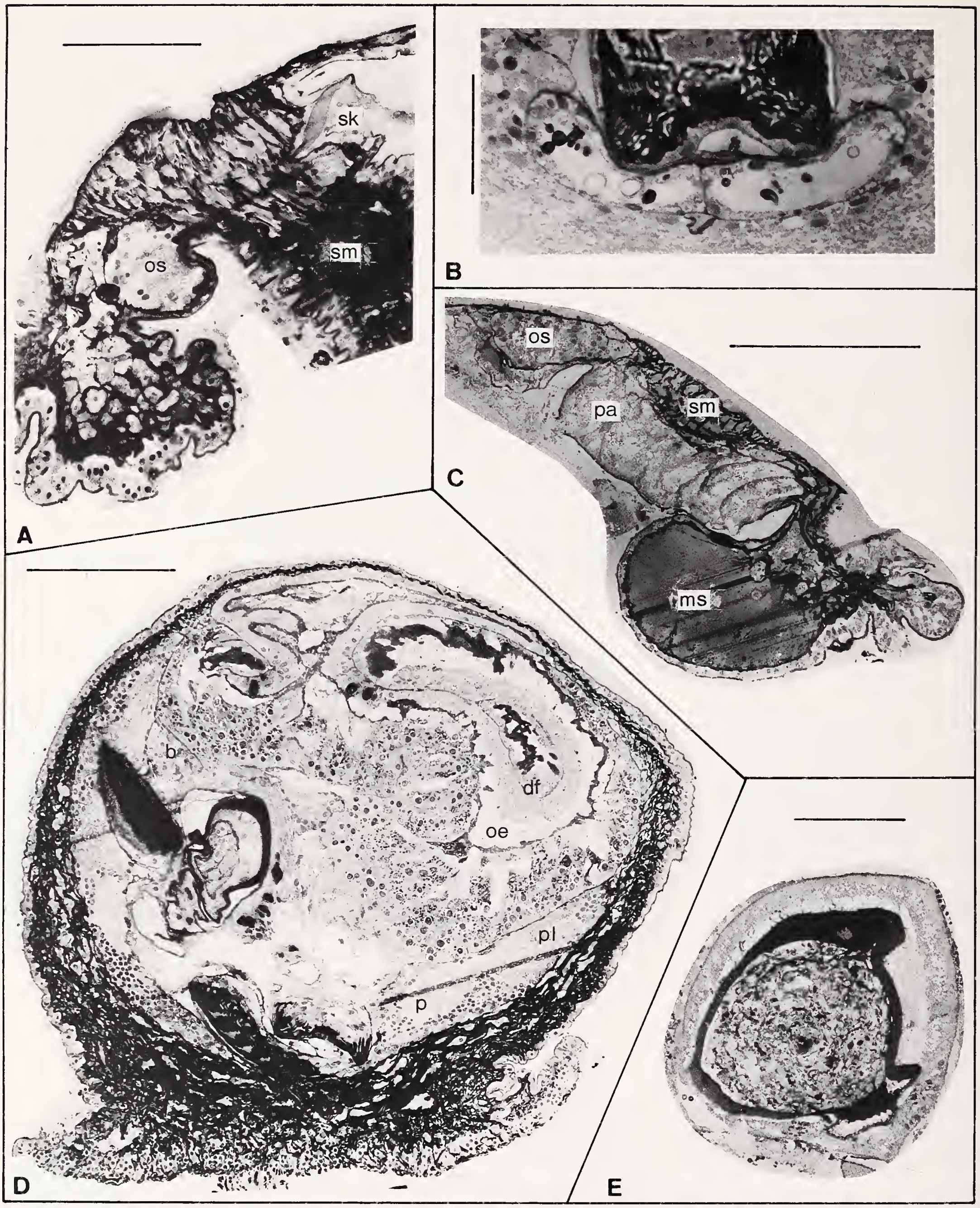

**Figure 2.** *Sutilizona theca* (USNM 859967, LACM 2355). Semi-thin sections of certain organs, all frontal view. **A.** Mantle margin near anterior end of right shell muscle. Note positions of osphradial ganglion and of the single ctenidial skeletal rod. Scale bar = 50 μm. **B.** Statocysts with statoconia. Scale bar = 25 μm. **C.** Mantle roof near anterior end of left shell muscle with pallial gland. Note positions of osphradial ganglion and of the single ctenidial skeletal rod. Scale bar = 100 μm. **D.** Voluminous anterior oesophagus with large dorsal folds, pleuropedal complex. Scale bar = 100 μm. **E.** Stomach with gastric shield filled with grit. Scale bar = 50 μm.

Lettering: b, buccal ganglion; df, dorsal oesophageal fold; ms, mantle sinus; os, osphradial ganglion; oe, lumen of anterior oesophagus; p, pedal ganglion; pa, pallial gland; pl, pleural ganglion; sk, skeletal rod of ctenidial axis; sm, shell muscle.

monopectinate ctenidia are unequal in several respects: The left gill reaches backwards to the anterior line of the pericard, its leaflets are rather long. Anteriorly left there is a prominent gland (Fig. 2C: pa). The right ctenidium is much smaller than the left one and occupies only the anterior half of the mantle cavity. The gill's axis is situated inwards of the right shell muscle and not at the mantle roof (Fig. 2A: sk), its leaflets are half as long as those of the left ctenidium, and the most anterior leaflets form a brush. The right ctenidial/osphradial ganglion (Fig. 2A: os) is situated to the right of the anterior end of the right shell muscle, whereas the left ganglion occupies the usual position inwards of the anterior end of the left shell muscle (Fig. 2C: sm). Each ctenidial leaflet bears a bursicle. Only the right hypobranchial gland is present, continuing the ctenidium backwards, and fills the free space of the right posterior mantle roof.

The diotocardian heart occupies the central and left mantle roof, its ventricle encloses the rectum. The left kidney lies in the pallial roof and has a simple opening to the left of the anus. The right kidney is much larger than the left one and forms large lobes centrally and to the left between the viscera. It contains many tiny excretory granules; the urinogenital opening is situated more posteriorly.

The species is gonochoristic; the male investigated is juvenile, the female investigated contains ripe eggs. In both sexes the gonad is very large and occupies the central body cavity, posteriorly it is situated at the left side. The appearance of the massive (not lobular) testis is granular, all stages of sperm development except ripe sperm cells are present. Late spermatocytes lack flagella. The vas deferens surrounds the stomach posteriorly, runs forward at the right dorsal side, and has a common opening with the right kidney. The ovary contains very large (max. 200 $\mu$m), yolky eggs in all stages of development. The course of the simple oviduct is as described for the vas deferens.

The jaws are massive and toothlike. The salivary glands are tubular and simple. A single pair of radular cartilages is present, the radular sheath is very long and makes an S-like loop. The anterior oesophagus (Fig. 2D: oe) is very broad, its dorsal folds and its glandular pouches are very large. The posterior oesophagus runs backward at the ventral right side and enters the stomach between the openings of the two unequal (the left one is smaller) midgut glands. The stomach is provided with a gastric shield (Fig. 2E) and sorting area, a caecum is not present. Like the intestine, which makes many loops, it is filled with grit and detritus (Fig. 2E).

The central nervous system of *Sutilizona* is hypoathroid (Fig. 2D: p, pl) and streptoneurous, the pedal cords are interconnected by several thin commissures. Generally all ganglia are very large, accordingly the connectives and commissures are short. The cephalic tentacles are smooth, a single pair of ESO-tentacles is present. The eyes are vestigial, consisting of a small vesicle lacking pigment, the optic nerve is still present. The statocysts contain many statocones that are hollow (Fig. 2B).

## FISSURELLACEA

### DIAGNOSIS

Vetigastropod limpets with shell slit or hole and two shell muscles, operculum present only in larval stage. Two ctenidia, hypobranchial glands restricted to the mantle-slit/hole area. Left kidney reduced; gonoduct opening into renopericardial duct of right kidney. Salivary glands enlarged, forming several tube like pouches. Anal gland may be present. Epipodial sense organs (ESO) at tips or at ventral sides of smooth tentacles. Eyes (if present) with closed vesicles.

### ANATOMY OF *CLYPEOSECTUS DELECTUS*, *C. CURVUS*, AND *PSEUDORIMULA MARIANAE*

#### Mantle Cavity

The mantle cavity is deep, more or less asymmetrical, and has a posterior, broad, triangular pouch at left and right (Fig. 3C: mc). In both *Clypeosectus* species the two bipectinate ctenidia are provided with long afferent and efferent membranes; anteriorly a short free axis is present, however. In *Pseudorimula* the ctenidial membranes are shorter so that the free portion is as long as the fused one. In both genera, each ctenidial filament has paired skeletal rods and a bursicle (Fig. 4G); the ctenidial axis also has paired skeletal rods corresponding to its bipectinate structure (compare with Temnocinclinae). An osphradium is situated inwards of the efferent membrane and at the free efferent axis of each ctenidium.

Conditions of the hypobranchial glands differ: In both sexes of *Clypeosectus* and in males of *Pseudorimula* these are small and are restricted to the mantle-slit area, whereas females of *Pseudorimula* lack a hypobranchial gland.

#### Heart and Excretory System

Whereas *Clypeosectus* species have a vestigial and isolated left kidney, this organ is lacking in *Pseudorimula*. Generally the right kidney is large and ramifies between the viscera, especially at the right side (Figs. 3C, 5A, C: rk). Both kidneys have their openings beneath the anus.

The heart is functionally diotocardian; the pericardium is very large. The auricles are of equal size but differ in shape (Figs. 3A–C: au, au').

#### Genital System

Clypeosectids are gonochoristic. The gonad is voluminous and occupies the posterior ventral part

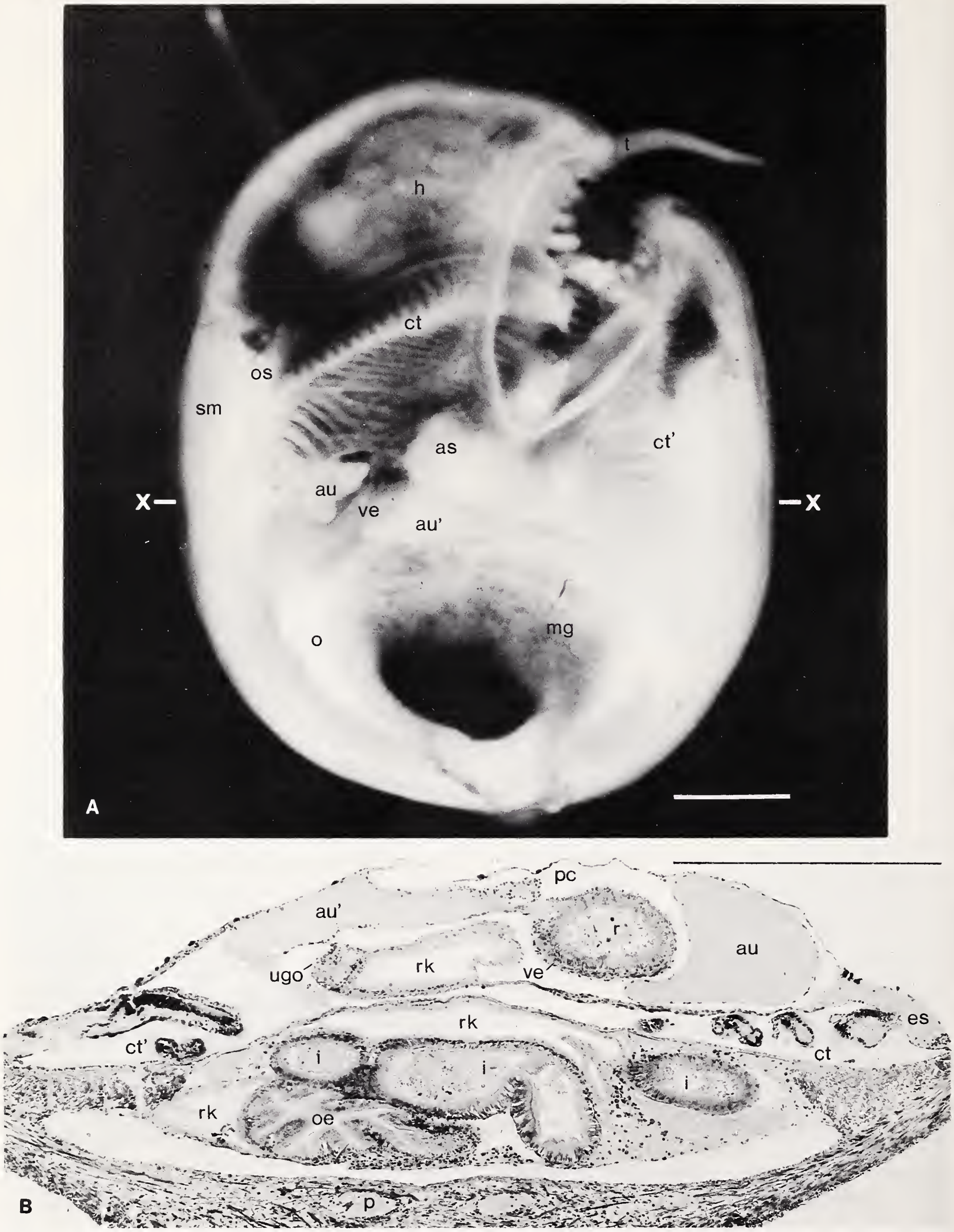

**Figure 3.** *Clypeosectus curvus*, female (LACM 2364a). **A.** Dorsal view of an intact specimen, shell removed. **B.** Section of the same specimen as marked in A. C. Reconstruction of mantle cavity and coelomic system of same specimen as in A and B. Scale bars = 500 $\mu$m.

Lettering: ag, anal gland; as, afferent ctenidial sinus; au, auricle; ct, ctenidium; es, efferent ctenidial sinus; h, head; i, intestine; lk, left (vestigial) kidney; mc, posterior end of mantle cavity; mg, midgut gland; o, ovary; od, oviduct; oe, oesophagus; os, osphradial ganglion; p, pedal cord; pc, pericardium; pd, reno-pericardial duct; r, rectum; rk, right kidney; rs, seminal receptacle; sm, shell muscle; t, cephalic tentacle; ugo, urinogenital opening; ve, ventricle.

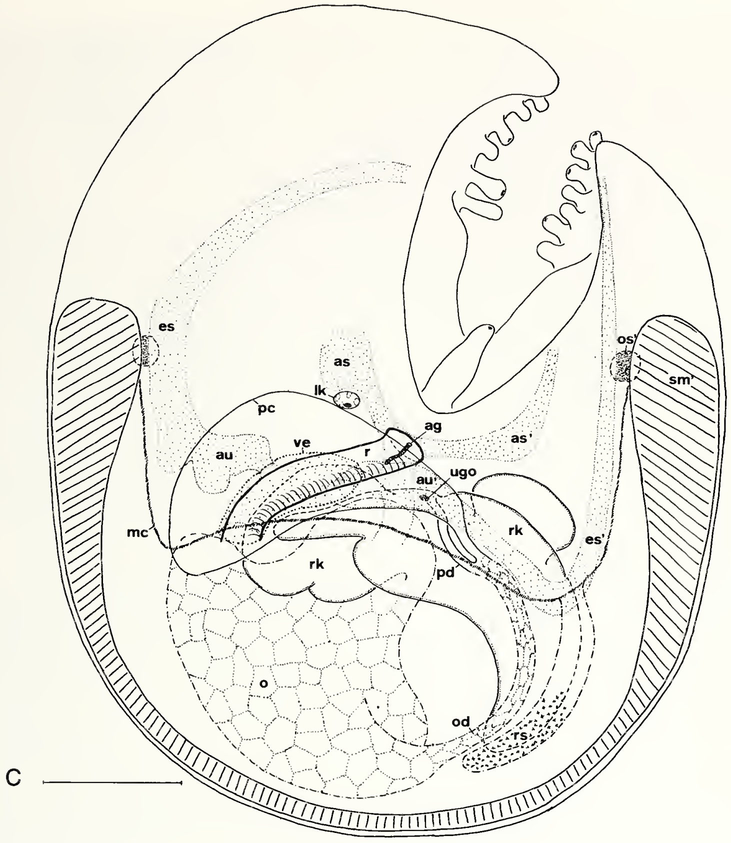

Figure 3. Continued.

of the visceral mass. In both sexes the gonoduct opens into the right renopericardial duct, which meets the right kidney near its opening (Fig. 3C: ugo).

The heads of the spermatozoa of *Clypeosectus* are about 6 μm long and filiform (Fig. 6B). In males these are found in great number in the proximal vas deferens, which is enlarged to form a fuctional vesicula seminalis. Ripe sperm cells also have been found freely in the mantle cavity of one female (Fig. 6B). In *Clypeosectus* a single, specific "prostate" gland (Fig. 5B: pr) is present, the epithelium of which is very high (50 μm) and consists of mucous cells and ciliated cells. It starts around the urinogenital opening. Here the right hypobranchial gland, which has a lower (30 μm), less ciliated epithelium, is enlarged and forms a distinct pocket. Posteriorly, the hypobranchial gland disappears and the prostate (Fig. 5C: pr) also forms a large pocket in the posterior right corner of the mantle cavity. From the anterior ventral prostate pocket a small but distinct ciliary band runs forward and over the right neck to the ventral base of the right cephalic tentacle, where the penis emerges. The latter has no groove or duct, but is densely ciliated. However, these structures are also present in the females of *Clypeosectus*. Here the ciliated band leads backwards to an otherwise isolated receptaculum seminis (Fig. 3C: rs), which opens into the most posterior extent of the mantle cavity on the right. Whereas the duct of the receptaculum has strong longitudinal folds (Fig. 4B: rs), the final vesicle lacks folds and is filled with sperm (Fig. 4C). The heads of these (probably allo-) spermatozoa are directed to the wall of the receptaculum vesicle (Fig. 4C). The oviduct is wide (100 × 35 μm) but depressed, and is simply ciliated. In the ovary all stages of egg development are present; ripe eggs are large (diameter 200 μm) and contain much yolk.

In males of *Pseudorimula* the prostate gland (Fig. 9C: rs) is paired and has the same histology as that of *Clypeosectus*. The left prostate gland forms a large pocket situated dorsally of the pericardium; the right prostate forms a large pocket at the posterior right corner of the mantle cavity, as in *Clypeosectus*. Here ripe sperm cells have been found that are in close contact with mucous droplets (Fig. 9C: md) of the prostate gland. Near this contact zone the droplets change their shape. The sperm cells (Fig. 9C: sp) have a round head (diameter about 4

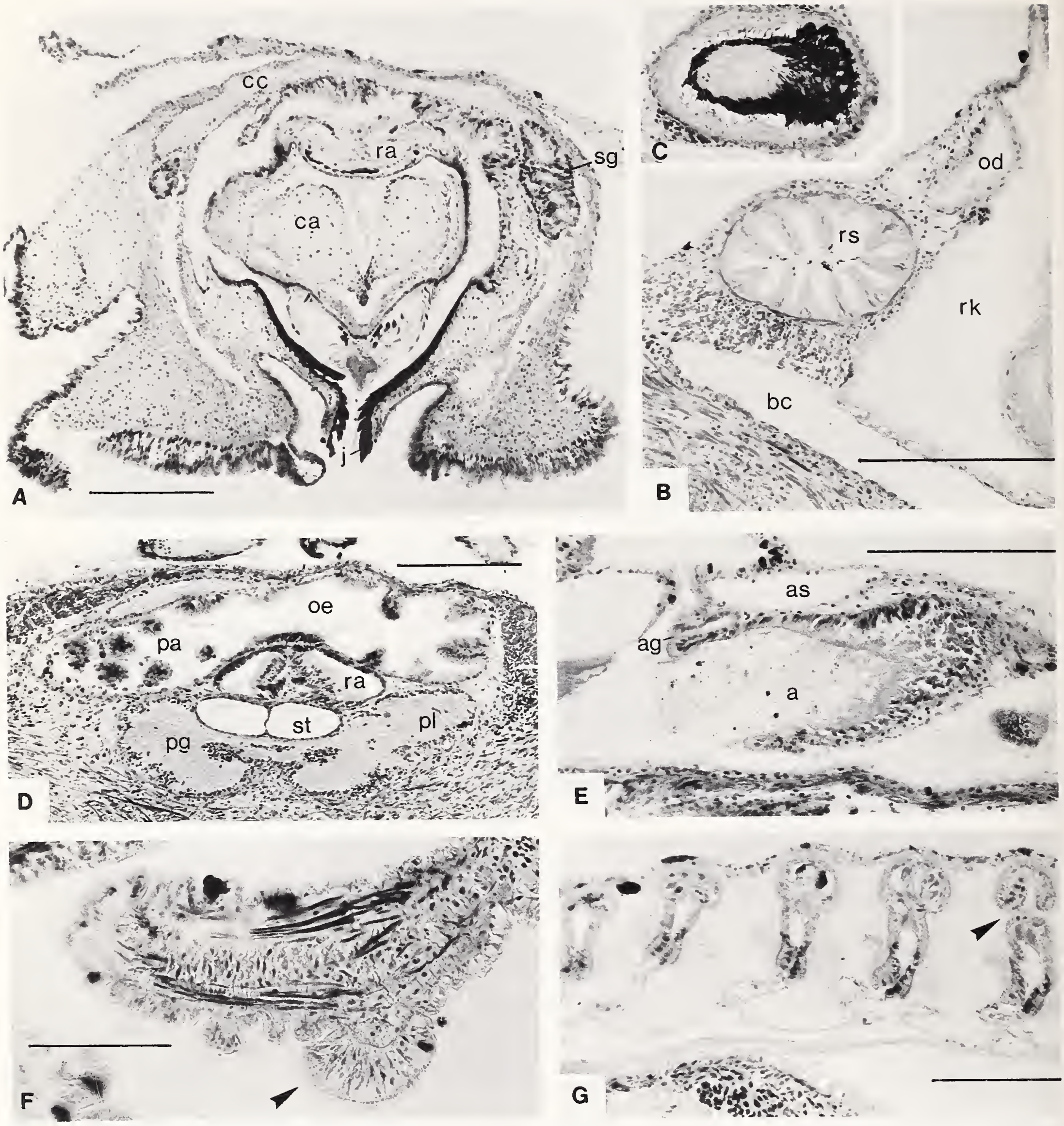

**Figure 4.** *Clypeosectus*, histological sections. **A.** *C. delectus* (holotype, female, USNM 859970), mouth opening. **B.** *C. curvus* (LACM 2364a), receptaculum duct with folded walls. **C.** *C. curvus*, same, posterior end of receptaculum with orientated sperm cells. **D.** *C. delectus*, statocysts. **E.** *C. curvus*, anus and anal gland. **F.** *C. curvus*, epipodial tentacle with ESO (arrow). **G.** *C. curvus*, ctenidial leaflets with bursicles (anterior to posterior is from right to left; arrow marks opening). Scale bars = A–D: 200 μm; E–G: 100 μm.

Lettering: a, anus; ag, anal gland; as, afferent ctenidial sinus (not yet divided into branches); bc, body cavity; ca, radular cartilage; cc, cerebral commissure; j, jaw; od, oviduct; oe, oesophagus; pa, oesophageal papillae; pg, pedal ganglion; pl, pleural ganglion; ra, radular sheath; rk, right kidney; rs, seminal receptacle (duct); sg, salivary gland; st, statocysts; ugo, urinogenital opening.

μm) and a rather short tail. Males of *Pseudorimula* lack a penis and the seminal groove.

The single investigated female of *Pseudorimula marianae* lacks a penis and a seminal groove, as well as a receptaculum. The conditions of oviduct and eggs are as described above for *Clypeosectus* (Fig. 3C); the ovary (Fig. 7: o) also fills the free space between the main muscle bundles.

### Alimentary Tract

The jaws of *Clypeosectus* are delicate, whereas those of *Pseudorimula* are massive (Fig. 8A: j), as in the

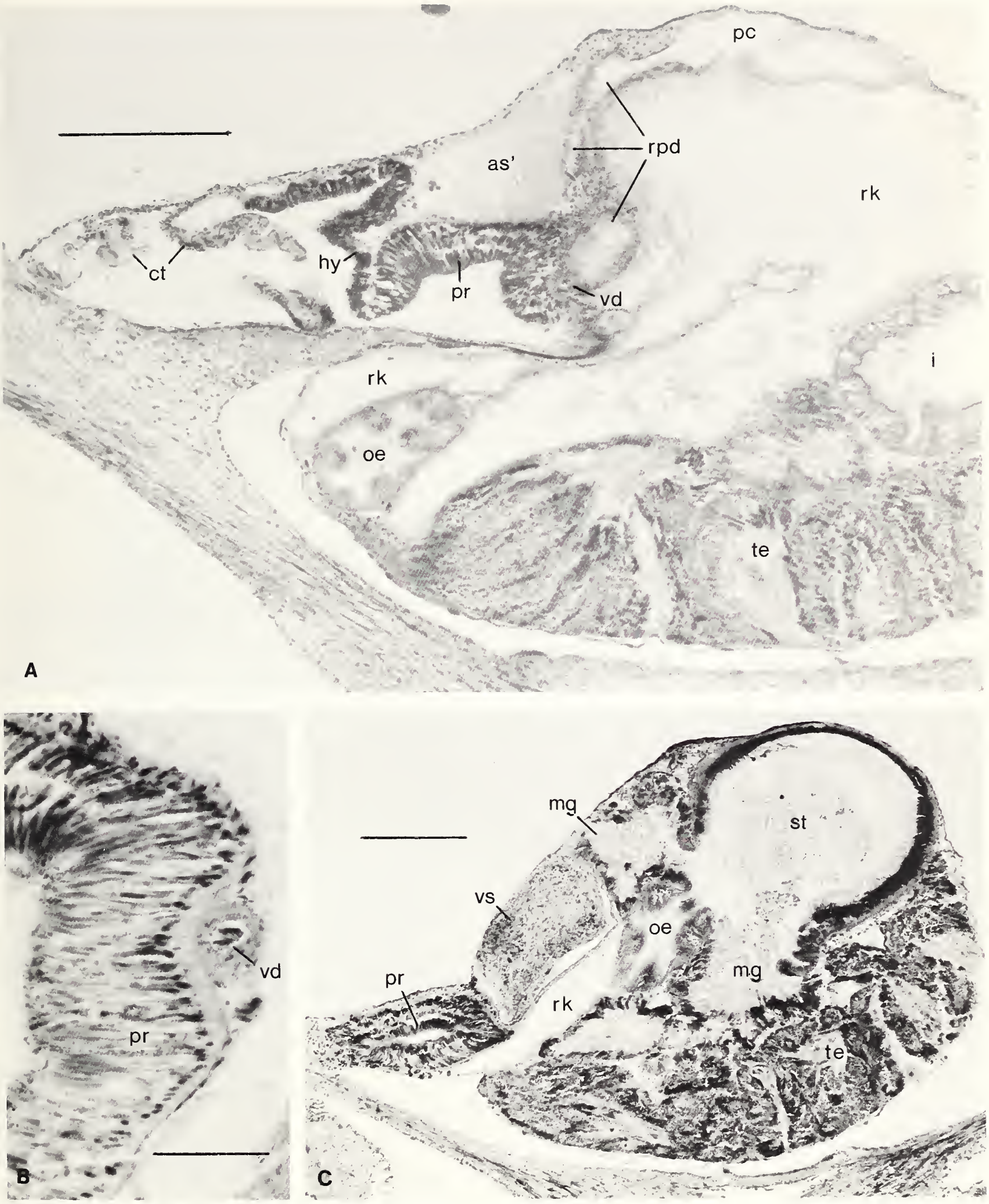

**Figure 5.** *Clypeosectus curvus,* male (LACM 2364b), histological sections. **A.** Posterior right mantle cavity and associated organs. Scale bar = 200 μm. **B.** Prostate and vas deferens. Scale bar = 50 μm. **C.** Posterior genital organs, openings of oesophagus and midgut glands into stomach.

Lettering: as, afferent ctenidial sinus; ct, ctenidial leaflets, hy, hypobranchial gland; i, beginning of intestine with groove; mg, midgut gland; oe, oesophagus, pc, pericardium; pr, prostate; rk, right kidney; rpd, reno-pericardial duct; st, stomach with gastric shield; te, testis; vd, vas deferens; vs, vesicula seminalis.

Temnocinclinae. Whereas the salivary glands of *Clypeosectus* are enlarged and form several tubelike pouches (Fig. 4A: sg), those of *Pseudorimula* form simple grooves (Fig. 8A: sg) continuing into the dorsal longitudinal folds of the oesophagus. In contrast to *Clypeosectus,* in which the posterior pair of radular cartilages is vestigial, these structures are well developed in *Pseudorimula* (Fig. 9A: ca1, ca2).

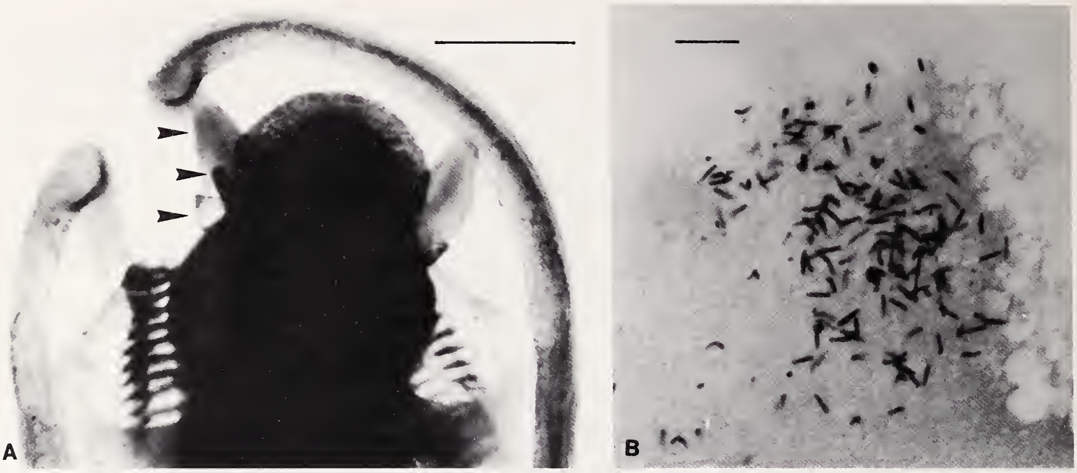

**Figure 6.** *Clypeosectus curvus,* male (LACM 2364b). **A.** Ventral view showing from anterior to posterior, cephalic tentacles, penis, and oral lappet (arrows). Scale bar = 1 mm. **B.** Ripe sperm cells (length 6 µm) from the mantle cavity of a female. Scale bar = 20 µm.

The radular sheath is short and straight and a radular caecum is lacking.

The anterior oesophagus has a specialized ventral tract; the oesophageal pouches more or less encircle the radula sheath and are papillate (Figs. 4D, 9A: pa). In *Clypeosectus* there is a continuous change into the posterior oesophagus, whereas in *Pseudorimula* the posterior oesophagus starts more abruptly, forming a dorsally positioned fold. The posterior oesophagus enters the stomach adjacent to the openings of the paired midgut gland (Fig. 5C: mg). The stomach itself is provided with a thick gastric shield; a protostyle and a spiral caecum could not be detected. The intestine makes several loops; like the stomach it has a distinct groove formed by a very thin epithelium. The rectum runs through the ventricle obliquely. In both genera these structures are filled with detritus, including iron sulfide particles, which destroyed several sections. In *Clypeosectus* a small anal gland (Fig. 4E: ag) opens adjacent to the right of the anus. In *Pseudorimula* an anal gland was not detected, but this is possibly due to some folds in the respective sections.

### Nervous System

The clypeosectid nervous system resembles that of the Scissurellidae (*e.g.,* Bourne, 1910) or the Fissurellidae (*e.g.,* Pelseneer, 1899). The anterior system is hypoathroid in having adjacent pleural and pedal ganglia (Figs. 4D, 9B: pg, pl). The cerebral ganglia are situated laterally at the bases of the cephalic tentacles and are interconnected by a very long commissure (Fig. 4A: cc). The labial lobe is small in *Clypeosectus,* large in *Pseudorimula;* a labial commissure could not be detected. There are pedal cords with several commissures. The visceral loop is streptoneurous and has distinct visceral ganglia. Two osphradial ganglia are present, corresponding to the number of ctenidia. As usual in archaeogastropods, the length of the visceral loop and the position of the visceral ganglion correspond to the depth of the mantle cavity (Haszprunar, 1988a).

### Sense Organs

Eyes are lacking. Whereas *Clypeosectus* species have retained an optical nerve, this is lacking in *Pseudorimula marianae.* Both genera show a dimorphism of epipodial tentacles (more appropriately ESO-tentacles). In the posterior (two or three) epipodial tentacles the ESO are situated at the tip (Fig. 8B), whereas the anterior (one or two) tentacles have them ventrally situated (Fig. 4F).

The paired osphradia are situated at the efferent ctenidial axes. A subradular organ is not present. The statocysts contain statoconia (Fig. 9B: st).

## DISCUSSION

## INFERRED MODE OF REPRODUCTION

### Scissurellidae

The scissurellid species described here anatomically are the only archaeogastropod inhabitants of the hydrothermal-vent habitat lacking all features of internal fertilization. Only the group-C limpets (Hickman, 1983; *i.e.,* the "symmetrical" limpets of McLean, 1985) also lack a penis or receptacula. Copulatory organs in males and/or receptacula in females have been described in all other archaeogastropods from the hydrothermal-vent habitat (McLean, 1981, 1985, 1988, 1989b; Fretter et al.,

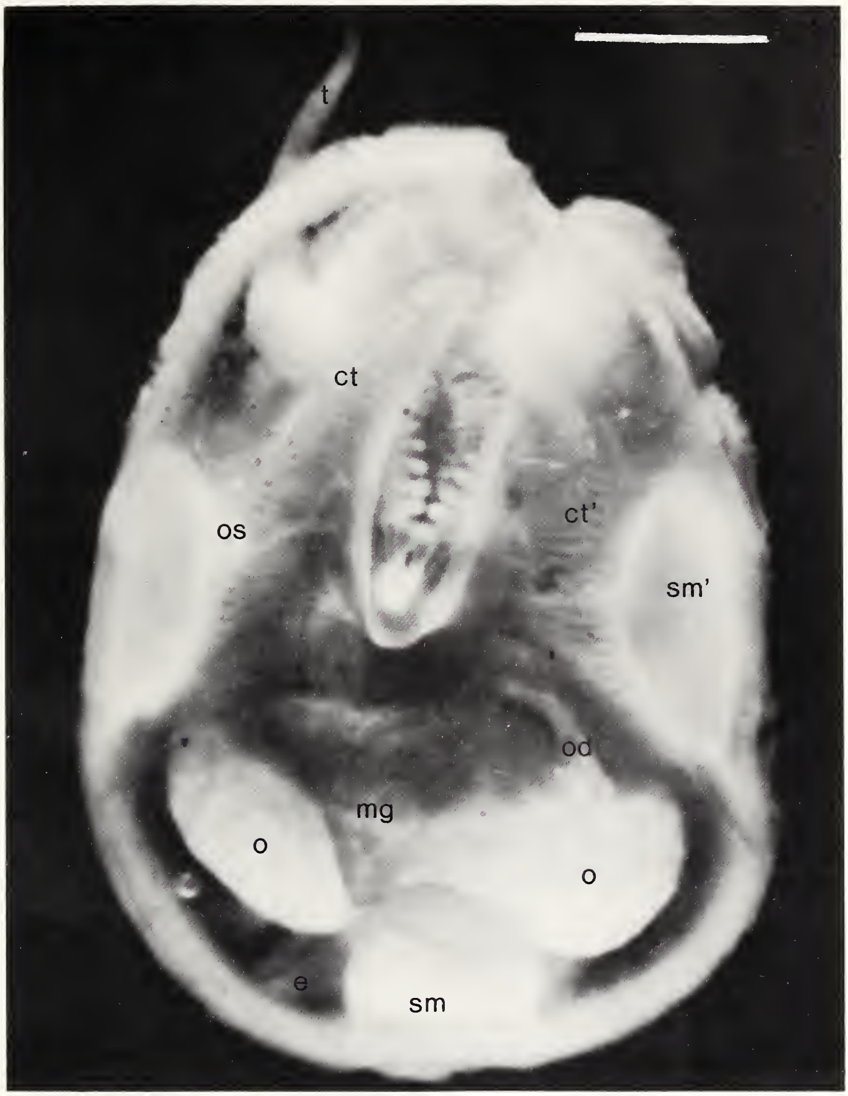

**Figure 7.** *Pseudorimula marianae,* female. Body of holotype (female, USNM 859977), dorsal view showing major details of organization. Scale bar = 1 mm.

Lettering: ct, ctenidium; e, epipodial tentacle; mg, midgut gland; o, ovary; od, oviduct; os, osphradium; sm, shell muscle; t, cephalic tentacle.

1981; Fretter, 1988; Warén and Bouchet, 1989; McLean and Haszprunar, 1987; Haszprunar, 1988a). Nevertheless, because of the small size of the animals, the obvious rarity of the animals (see McLean, 1989b), the structure of the sperm cells (lacking long flagella), and the low number of eggs, it is likely that fertilization takes place in the female mantle cavity. This might likewise be correct for other scissurellid species; however, the mode of sperm transfer is completely unknown in the Scissurellidae.

Obviously, males of the rift-vent scissurellid species occur as close as is possible to 50% (3 of 5 determined specimens). This is in contrast to certain shallow-water species, where males are very rare (*Incisura:* Bourne, 1910: 16; *Scissurella:* Marietta Strassoldo, pers. comm., July 1988). Possibly facultative parthenogenesis takes place in such species. As a whole, fertilization biology of the Scissurellidae may be much more complex than previously thought.

## Clypeosectidae

As far as is known, *Clypeosectus* is the only zeugobranch genus with internal fertilization via a penis. Based on anatomy, the probable route of

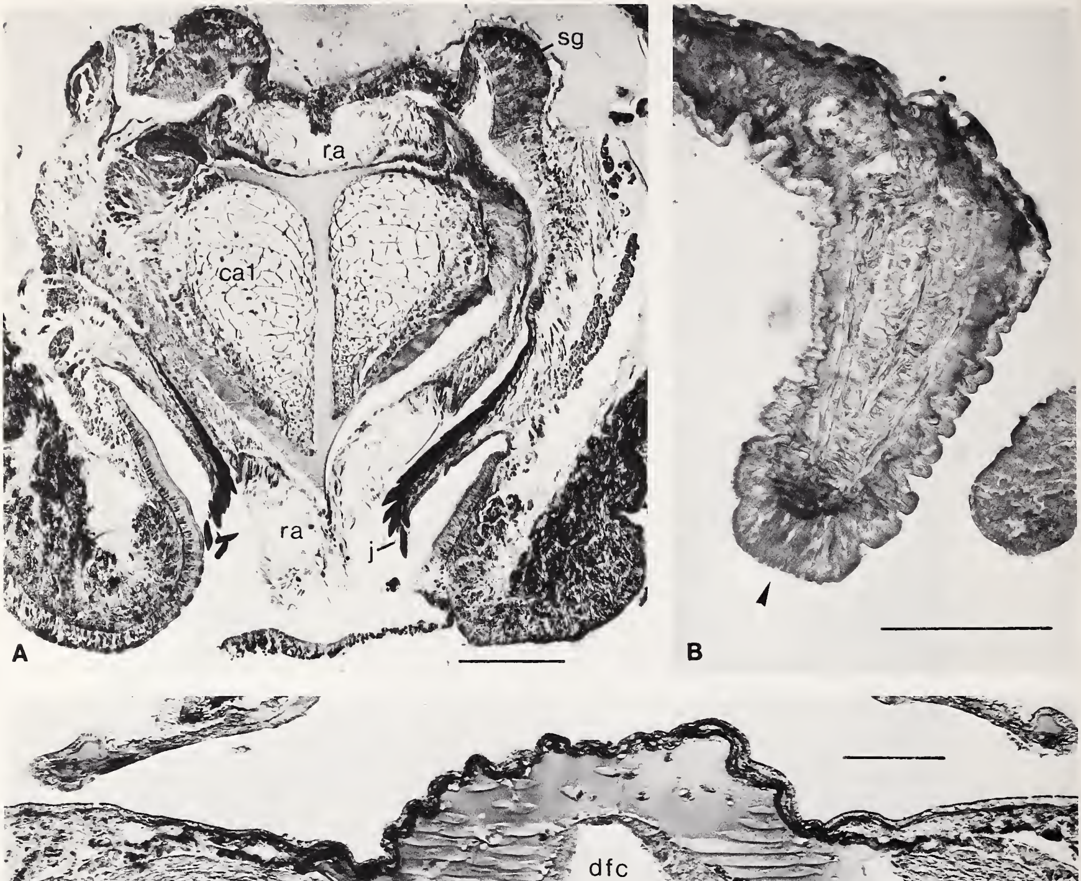

**Figure 8.** *Pseudorimula marianae,* histological sections, all frontal views. All scale bars = 100 μm. **A.** Buccal cavity and mouth opening of male (LACM 2366a). **B.** Posterior epipodial tentacle of holotype (female, USNM 859977) with ESO (arrow) at tip. **C.** Cerebral ganglia and anterior oesophagus of holotype (female).

Lettering: c, cerebral ganglion; ca1, anterior radular cartilage; dfc, dorsal food channel; j, jaw; oe, oesophagus; oep, oesophageal pouch; ra, radula; rs, radular sheath; sg, salivary gland.

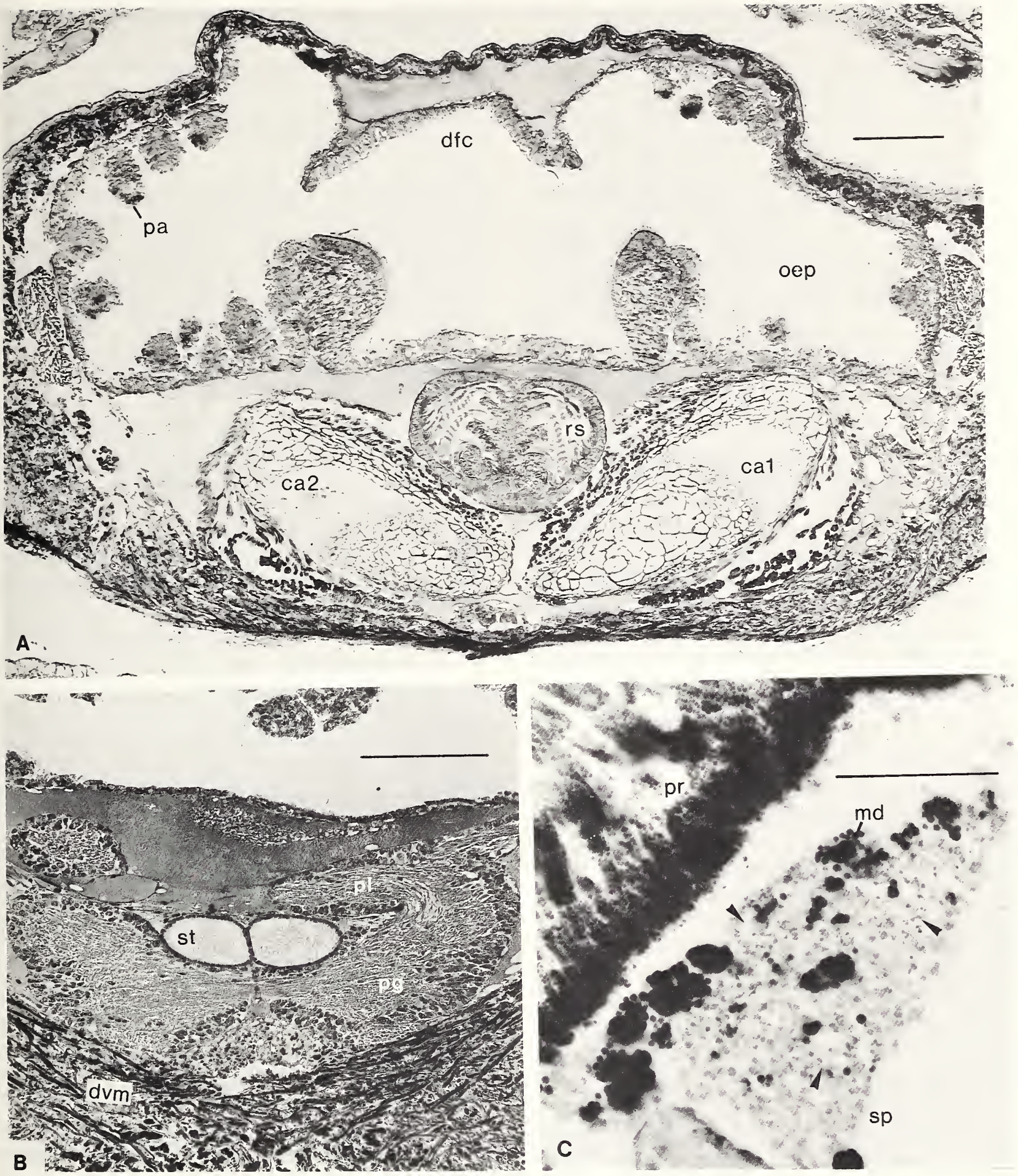

**Figure 9.** *Pseudorimula marianae,* histological sections, all frontal views. **A.** Radular cartilages and anterior oesophagus of holotype (female, USNM 859977). Scale bar = 100 μm. **B.** Intercrossed dorso-ventral (shell) muscles, pleuropedal complex, and statocysts of male (LACM 2366a). Scale bar = 50 μm. **C.** Mantle cavity of male. Prostate gland and free sperm with prostate mucous droplets, which are larger than those in the mucous cells of the prostate gland and successively desintegrate (arrows). Scale bar = 50 μm.

Lettering: ca1(2), anterior (posterior) radular cartilage; dfc, dorsal food channel; dvm, dorsoventral (shell) muscles; md, prostate mucous droplets; oep, oesophageal pouch; pa, oesophageal papillae; pg, pedal ganglion; pl, pleural ganglion; pr, prostate gland; rs, radular sheath; sp, sperm cells; st, statocyst.

gametes in *Clypeosectus* is as follows: Ripe spermatozoa are stored in the seminal vesicle, then pass via the vas deferens and the right renopericardial duct, and finally are released through the urinogenital opening into the mantle cavity. The mucus of the prostate gland probably packs the sperm cells together; they are transferred via the seminal groove and the penis into the mantle cavity of the female. There the sperm cells are stored in the receptaculum seminis. When eggs are released via the oviduct, renopericardial duct, and urinogenital opening, sperm cells become free and fertilization takes place in the mantle cavity of the female. Brood protection may occur, as in many Cocculiniformia (see Haszprunar, 1988b), but is unknown at present.

A puzzling question concerns the "copulatory" process and a "seminal" groove that is also present in females of *Clypeosectus*. These structures could be used in egg-laying, as assumed for the neritacean genus *Phenacolepas* Pilsbry, 1891, by Fretter (1984), or may simply be the result of genetic interference (expression of male genes in females) between the sexes. Protandric hermaphroditism is very unlikely, considering that the single male is fully mature. Correspondingly, a similar condition occurs in the Lepetodrilidae (Fretter, 1988, and pers. obs.), in which females have a copulatory process that is smaller, as well as a groove in the position of the seminal groove of males.

Obviously the conditions in *Pseudorimula* (lack of copulatory process in males, and lack of receptaculum seminis in females) are less specialized and more primitive. However, the presence of quite aberrant sperm and of a large prostate gland also suggest internal fertilization in this genus. The exact influence of the prostate on the sperm cells and the mode of sperm-transfer (via mobil spermatophores?) is completely unknown at present. Medem (1945) reported sperm in the mantle cavity of *Fissurella nubecula* (Linnaeus, 1758) (see also Fretter and Graham, 1962:324) and this condition may be typical for the Fissurellacea, as there is as yet no report on external (free water) fertilization of any fissurellid. Thus, fissurellids and both clypeosectid genera seem to reflect a step by step process toward internal fertilization via a penis.

## GENERAL REMARKS ON PHYLOGENETICS

The following considerations are based on an assumed vetigastropod archetype (= stem species), which is characterized as follows (for reasoning see Haszprunar, 1988a, and in prep.): Shell small (2–4 mm), coiled, with few whorls and slit; protoconch I (= embryonic shell) with more or less regular sculpture. Operculum in adults present, a single pair of cephalic and few pairs of epipodial tentacles provided with papillae, a single pair of (smooth) tentacles with ESO. Mantle cavity deep; two bipectinate ctenidia (left one slightly larger) with long efferent and short afferent axial membranes, the leaflets provided with bursicles; two osphradia; two hypobranchial glands. Heart diotocardian, auricles of equal size and of different shape, the ventricle encircles the rectum. Two kidneys with different structure and function, the left one at the pallial roof, the right one ramifying between the viscera, both connected with the pericardium. Sexes separate, the ciliated gonoduct (vas deferens or oviduct) and the right renopericardial duct have a common urinogenital opening. Sperm of the primitive type, eggs large and lecithotrophic, external fertilization. Paired jaws consisting of numerous teeth, salivary glands are simple pouches. Radula rhipidoglossate, symmetrical; two pairs of cartilages and a radular diverticulum present. Anterior oesophagus of the polyplacophoran type, with papillate pouches, more or less encircling the buccal apparatus, showing torsion. Stomach provided with gastric shield, protostyle, and simple caecum; paired midgut gland; intestine with few loops; rectum through heart. Nervous system hypoathroid, long cerebral commissure, with labial ganglia and commissure, pedal cords interconnected by several commissures, visceral loop streptoneurous. Eyes open, with lens; statocysts with several statocones.

## ANATOMICAL COMPARISON OF SCISSURELLID SPECIES

The anatomies of *Temnocinclis euripes* and *Temnozaga parilis* are very similar. Aside from shell and radula characters (see McLean, 1989b), both species differ only in the anterior oesophagus (papillate or not) and in epipodial features. Obviously both genera are closely related. In contrast, *Sutilizona theca* is quite different in anatomy and radula and thus not closely related to either.

The scissurellid nature of all three species is founded on the characters of shell, radular, epipodial, and sperm conditions. According to the assumed vetigastropod archetype (see above), most of these characters are primitive for Vetigastropoda (shell slit, symmetrical radula, epipodium with few epipodial and a single pair of ESO-tentacles), or might be due to convergence (lack of nacre, derived sperm cells). Thus, the scissurellid nature of Temnocinclinae and Sutilizoninae is poorly founded, nevertheless it is the most probable solution. Further studies on shell structure (see Batten, 1975) or sperm ultrastructure (see Healy, 1988) should substantiate the present classification.

Although the extent of anatomical variation is poorly known in the Scissurellidae, differences from other scissurellids can be summarized as follows:

(1) *Temnocinclis euripes* and *Temnozaga parilis* differ from other scissurellids (including *Sutilizona theca*) in having a nearly symmetrical shell and mantle cavity, diagnostic radular features (McLean, 1989b), two monopectinate ctenidia of equal shape and position, lack of eyes, and in the particular structure of the statocyst. Further common characters (although not unique among the Scissurellidae) are the smooth cephalic and epipodial tentacles, the presence of both hypobranchial glands, the type of salivary glands, and the unusual sperm cells. According to these common characters of *Temnocinclis* and *Temnozaga* both genera are united in a new subfamily Temnocinclinae among the Scissurellidae (McLean, 1989b).

(2) *Sutilizona theca* differs from other Scissurellidae (including the Temnocinclinae) in having a unique protoconch sculpture, a diagnostic radula (McLean, 1989b), a single pair of radular cartilages, a very broad anterior oesophagus, a multi-looped

intestine, the left pallial gland, the large gonads (otherwise restricted to the left body cavity; *e.g.*, Bourne, 1910), and vestigial eyes. Further diagnostic (but not unique among the Scissurellidae) features are the monopectinate ctenidia, the single (right) hypobranchial gland, the type of salivary glands, and the sperm cells. In accordance with McLean (1989b), I regard the differences mentioned above as important enough to place *Sutilizona theca* in its own subfamily, Sutilizoninae. The occurrence of a single pair of ESO-tentacles might be explained by the immaturity of the specimens studied (see McLean, 1984: fig. 6), although McLean (1989b) noted that the foramen is closed, which is indicative of maturity. Thus, *Sutilizona theca* may exhibit a paedomorphic condition in this respect.

It is uncertain whether Temnocinclinae and Sutilizoninae are sister-groups (for their scissurellid nature see above), and whether or not both groups have invaded the hydrothermal-vent habitat independently. The similarities of both subfamilies (reduction of eyes, monopectinate ctenidia, smooth tentacles) might be due to convergence, because all these characters are also found in other deep-water or hydrothermal-vent vetigastropods. The lack of the enlarged forth lateral tooth might be a commonly derived character (McLean, 1989b); however, the buccal apparatus of *Sutilizona theca* differs considerably from that of the Temnocinclinae and other scissurellids. Moreover, the remaining anatomy of both subfamilies differs considerably. Therefore a sister-group relationship of Temnocinclinae and Sutilizoninae is possible but not yet ascertained.

## STATUS OF SCISSURELLIDAE (SCISSURELLACEA)

Until now the Pleurotomariacea (*sensu lato*) have been exclusively defined by primitive characters, suggesting that the group represents a grade rather than a clade.

Pleurotomariidae and Trochacea are closely allied by sharing the oviductal gland (Bourne, 1910; Fretter, 1966). The Haliotidae stand closer to both families than to Scissurellidae in also having a posteriorly elongated mantle cavity and a spiral caecum of the stomach. As noted by Bourne (1910:31): "Not only are the Scissurellidae distinct from the Pleurotomariidae, but they are clearly less closely related to them than the Haliotidae or even than the Trochidae and Turbonidae [sic], for the last-named families, although they have lost the labral incision in the shell, as also the right ctenidium and the structures correlated to it, have retained many anatomical features which find their counterpart in *Pleurotomaria.*" In addition, the Scissurellidae exhibit a quite different and advanced sperm ultrastructure, whereas the Pleurotomariidae and Haliotidae have sperm of the primitive type (Healy, 1988; this paper).

These considerations suggest that the "Pleurotomariacea" (comprised of Pleurotomariidae, Haliotidae, and Scissurellidae) very probably represents what Haszprunar (1986) has called a multidimensional paraphyletic group (*i.e.*, a grade with two or several emerging lines not included), because the Fissurellacea and Trochacea, and possibly also the Lepetodrilacea (see Haszprunar, 1988a), are here considered to have branched off at different points along the "pleurotomariacean" line. As outlined in detail by Haszprunar (1986), such groups must be dissolved, otherwise the hypothesized phylogenetic relationships cannot be expressed unequivocally in a classification. Superfamilial status for the Haliotidae has already been proposed by Golikov and Starobogatov (1975), so that only the Scissurellidae remain to be removed from the Pleurotomariacea. Accordingly, the family Scissurellidae is elevated to superfamilial level in this paper. This is well founded, considering the numerous differences summarized by Bourne (1910:30) and outlined herein.

The restriction of Pleurotomariacea to the Pleurotomariidae does not take into account 20 extinct Paleozoic and Mesozoic taxa treated by paleontologists at the family level within the Pleurotomariacea, all of which have conispiral shells with slits or hole series, differing in size and other characters of shell morphology from the Pleurotomariidae (see Knight et al., 1960). Living Pleurotomariidae have a rhipidoglossate radula unlike that of other vetigastropods (see Hickman, 1984a,b), differing to the extent that some authors designate it as "hystrichoglossate" rather than rhipidoglossate. In contrast, the radulae of Haliotidae and Scissurellidae are more typical of other vetigastropods. The hystrichoglossate radula may well be a novelty of the family Pleurotomariidae, which dates from the Mesozoic, as do the Haliotidae and Scissurellidae. It is much more likely that the ancestors of the latter two families were conispirally coiled "pleurotomariaceans" with typical kinds of rhipidoglossate radulae, rather than that the ancestors had the hystrichoglossate radula. Accordingly, it is much more likely that some or all of the extinct families might have had the basic features of scissurellacean organization, except for such derived features as an advanced shell structure that includes loss of nacre. It is likely that anatomy of the extinct families would therefore place them in the Scissurellacea, rather than in the Pleurotomariacea (*sensu stricto*).

According to Knight et al. (1960) the Scissurellidae first appeared in the fossil record during the Cretaceous. Earlier fossils from the Triassic have been recently discovered (K. Bandel, pers. comm., Sept. 1988), placing the origin of Scissurellidae early in the Mesozoic. The scissurellid body plan, however, is likely to have had a Paleozoic origin.

## ANATOMICAL COMPARISONS OF CLYPEOSECTID SPECIES

Several characters of *Pseudorimula* differ from those of *Clypeosectus* both in external and internal organization. Differences concern external shape, presence of copulatory processes, shell muscle, length of the ctenidial membranes, genital system, salivary glands, radular cartilages, oesophagus, size of labial lobe, presence of optic nerve, and number of ESO-tentacles. The phylogenetic significance of these differences is treated further below.

Inclusion of the Clypeosectidae in the Vetigastropoda is based on the shell slit, the presence of epipodial sense organs, the number (two) and type of ctenidia (bipectinate with skeletal rods and bursicles), and the oesophageal conditions (papillate pouches encircling the radular sheath).

The fissurellacean affinity of Clypeosectidae is based upon essential features in the excretory, reproductive, and digestive systems. The vestigial left kidney is a basic feature of the Fissurellidae, otherwise known only in the lepetellacean family Pyropeltidae (McLean and Haszprunar, 1987). In the genital system, the gonoduct opens into the renopericardial duct, reaching the right kidney near its opening, which is a basic character of the Fissurellidae, although present in the Lepetodrilacea (Fretter, 1988). In *Clypeosectus,* the salivary glands consisting of several pouches, and the presence of an anal gland, are typical fissurellacean characters that are not found in any other archaeogastropod group. Moreover, the ESO are situated at the ventral base of the epipodial tentacles as in fissurellids, a condition otherwise known only in Haliotidae. In addition, the rather small hypobranchial glands are restricted to the shell-slit area, as in fissurellids.

Differences from the Fissurellidae include the shell shape (more markedly asymmetrical), lack of shell pores, double anterior edge of foot marking pedal gland (absent in adult Fissurellidae), shell muscle (no hooks), cephalic tentacles (smooth), epipodium (few tentacles instead of many), internal fertilization (unknown in Fissurellidae), and particularly the radular characters (symmetrical plan, no enlarged fifth lateral as in Fissurellidae), lack of radular caecum, and the lack of a subradular organ.

Clypeosectids resemble the Temnocinclinae in having three posterior pairs of epipodial tentacles, the double anterior edge to the foot, and similar transparency to the shell. However, clypeosectids lack an operculum, the epipodial and cephalic tentacles are longer than those of the Temnocinclinae, and the additional genital process in both sexes is lacking in the latter. Whereas the similarities are regarded as common primitive characters for the Vetigastropoda (see above), the differences in anatomy indicate that the Temnocinclinae and the Clypeosectidae belong to different superfamilies.

## STATUS OF CLYPEOSECTIDAE

The status of the Clypeosectidae as a clade appears well founded by several pecularities of the family. The most important are the common aberrant radula type, the common modifications of the male genital system (prostate gland), and the shared epipodial condition. Accepting this view, all similarities shared by only one genus with the Fissurellidae must be due to convergence, or reflect a common basal condition in the Fissurellacea.

Such similarity is found in the salivary glands. Whereas *Clypeosectus* has several pouches as in the Fissurellidae, *Pseudorimula* has only simple ridges. Among archaeogastropods reduction of the salivary glands has been reported in the Cocculinidae and certain genera of the Pseudococculinidae (Haszprunar, 1988b). In contrast, the condition of *Clypeosectus* and the Fissurellidae is unique. It is thus more likely that the salivary gland of *Pseudorimula* represents the advanced state among the Fissurellacea.

A second case is the symmetry of shell and mantle cavity in *Pseudorimula* and Fissurellidae. One could speculate that this genus represents an intermediate level between the marked asymmetry of *Clypeosectus* and the nearly perfect symmetry in the Fissurellidae. However, this idea would imply that Clypeosectidae is a grade rather than a clade and that the above-mentioned pecularities of the family are convergences or primitive ones. That they are both is highly improbable. The logical conclusion is therefore that the symmetrical conditions of *Pseudorimula* and Fissurellidae have been convergently evolved. This is much more likely because there are several cases of secondary symmetry known among gastropods (see Yonge, 1947).

Comparison with the vetigastropod archetype (see above) indicates that within the Clypeosectidae, *Clypeosectus* is more advanced with respect to the following characters: copulatory processes in both sexes, the asymmetry of the prostate glands, the presence of a receptaculum in females, the larger degree of fusion of the ctenidial axis, the reduction of the posterior pair of radular cartilages, and the smaller labial lobe. In *Pseudorimula* the general symmetry, the sperm cells, the salivary glands and oesophageal conditions, and the loss of the optical nerve are advanced characters.

## STATUS OF FISSURELLACEA

The Fissurellacea clearly represent a clade (Haszprunar, 1986, 1988a). Shared derived characters are the excretory system with a reduced left kidney and the anal gland. Also the genital system, in which the gonoduct opens directly into the renopericardial duct, is distinctly modified from the primitive condition. This condition, however, also occurs in the Lepetodrilacea (pers. obs.). In addition, the salivary glands typically form several pouches. Finally the operculum has been lost in the adult, although this is correlated with limpet life. Modifications of the epipodium are of minor importance, as a similar position of the ESO-tentacles also occurs in Haliotidae (see Crofts, 1929).

In still having an asymmetrical shell and mantle cavity and a pedal gland, *Clypeosectus* stands close to a hypothetical fissurellacean ancestor. Specialization concerns the radular type, lack of eyes, and internal fertilization. In contrast, the Fissurellidae have developed a special caecum of the radular sheath (Fretter and Graham, 1962: fig. 96: pdm), lost the pedal gland in adults, and developed a more symmetrical shell and mantle cavity.

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Natural History Museum
of Los Angeles County
900 Exposition Boulevard
Los Angeles, California 90007

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## PHYLOGENY AND BIOGEOGRAPHY OF THE MARINE ISOPOD FAMILY CORALLANIDAE (CRUSTACEA, ISOPODA, FLABELLIFERA)

PAUL M. DELANEY

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[1] Life Sciences Division, Los Angeles County Natural History Museum, 900 Exposition Boulevard, Los Angeles, California 90007.
Current address: Division of Science and Mathematics, University of the Virgin Islands, Charlotte Amalie, St. Thomas, U.S. Virgin Islands 00802, U.S.A.

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**ABSTRACT.** Isopod crustaceans of the marine family Corallanidae (Flabellifera) were examined using light and electron microscopy. Type-species, type-specimens, and non-type material for each of the six corallanid genera were used to prepare new (revised) generic diagnoses and additional descriptions. The genus *Austroargathona* was synonymized with *Tachaea.*

A matrix of external morphological characters was developed for the corallanid genera and the outgroups Tridentellidae and Cirolanidae. This character matrix was analyzed with the cladistic computer program PAUP (Swofford, 1985) and the program package PHYLIP (Felsenstein, 1984); PHYLIP programs used included WAGNER, PENNY, DOLLOP, MIX (Camin-Sokal option), and CLIQUE. Fifty trees derived from these programs were compared for topology and tree length. Homoplasy statistics, if provided by the program, were also compared. A single PAUP tree produced using "unordered" characters was determined to be the most parsimonious tree; it was the shortest tree, with the lowest homoplasy, and with the topology most corroborated by trees from other programs. This tree was considered the best estimate of cladistic relationships (genealogy) among the corallanid genera.

Limited congruence between a proposed cladogram of tropical ocean areas and a taxon-area cladogram derived from cladistic analysis supports the hypothesis that divergence of the Corallanidae from the Tridentellidae was related to the opening of the Atlantic and Indian Oceans. The Corallanidae are hypothesized to have evolved from ancestors present in a circumtropical warm-water Tethyan-track fauna, with modern genera existing prior to the Pliocene.

**RESUMEN.** Los crustáceos isópodos marinos de la familia Corallanidae (Flabellifera) fueron examinados usando microscopía de luz y electrónica. Se examinaron especies tipo, especímenes tipo, y material no tipo de cada uno de los seis géneros coralánidos para preparar nuevas diagnosis genéricas (revisadas) y descripciones adicionales. El género *Austroargathona* fue sinonimizado con *Tachaea.*

Se desarrolló una matriz de caracteres morfológicos externos para los géneros coralánidos y los grupos externos Tridentellidae y Cirolanidae. Esta matriz de caracteres fue analizada con el programa de computación cladístico PAUP (Análisis Filogenético usando Parsimonia) (Swofford, 1985) y la colección de programas PHYLIP (Felsenstein, 1984); los programas PHYLIP usados incluyen WAGNER, PENNY, DOLLOP, MIX (opción Camin-Sokal), y CLIQUE. Se compararon topología y longitud de cincuenta cladogramas derivados de estos programas. Se determinó que un solo cladograma PAUP producido usando caracteres "desordenados" era el mas corto, con la homolasia mas baja y con la topología mas corroborada por cladogramas de otros programas. Se considera que este cladograma es la mejor estima de las relaciones cladísticas (genealogia) entre los géneros coralánidos.

La hipótesis de que la divergencia de Corallanidae y Tridentellidae estuvo relacionada con la apertura de los Océanos Atlántico e Indico es sostenida por la congruencia limitada existente entre un cladograma de áreas oceánicas tropicales propuesto y un cladograma taxon-area derivado de análisis cladístico. Se hipotetiza que los Corallanidae han evolucionada desde ancestros presentes en una fauna del Mar de Tethys, característica de aguas cálidas circumtropicales, con géneros modernos que existen desde antes del Plioceno.

## INTRODUCTION

The Isopoda is one of nine orders of peracarid Crustacea. There are nine suborders of Isopoda, including the Flabellifera. Within the Flabellifera there are 13 families, including a group of five families that superficially resemble one another and are presumably closely related; these are the Cirolanidae, Tridentellidae, Corallanidae, Aegidae, and Cymothoidae. These families are thought to make up an "ecological and phylogenetic lineage" trending from a free-living, scavenging-predatory lifestyle in the Cirolanidae to a parasitic and specialized existence in the Cymothoidae (Menzies et al., 1955; Brusca, 1981). The Corallanidae have been collected as both free-living and "parasitic," and show many morphological adaptations toward an increasingly parasitic lifestyle. The Corallanidae are thought to occupy a position between the Tridentellidae and Aegidae in the evolutionary lineage above (Brusca, 1981; Delaney, 1984).

This study concerns the Corallanidae and consists of three sections: 1) the systematics of the family and its six component genera; 2) a genus-level cladistic analysis, using two related families from the evolutionary lineage (above) as out-groups; and 3) a phylogenetic and historical biogeographic analysis of the family.

## SYSTEMATICS

### MATERIALS AND METHODS

Specimens were obtained via field collections and bulk loans from various museums around the world. A complete list of museums from which specimens were borrowed during this study, with the abbreviations for them used herein, follows:

AHF—Allan Hancock Foundation, University of Southern California, Los Angeles, California
AM—Australian Museum, Sydney
BMNH—British Museum (Natural History), London
CAS—California Academy of Sciences, San Francisco, California
LACM—Los Angeles County Museum of Natural History, Los Angeles, California
NTM—Northern Territory Museum, Darwin, Australia
SAfM—South African Museum, Cape Town
USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMHUB—Museum für Naturkunde der Humboldt-Universitat zu Berlin
ZML—Zoological Museum, Leiden, Netherlands (Rijksmuseum van Natuurlijke Historie)
ZMUC—Zoologiske Museum, University of Copenhagen, Denmark

Other abbreviations used in the Materials Examined sections include: coll. (collected by), fe. (female), ma. (male), and spec. (specimens).

Gross morphology of specimens was studied via dissection and examination using a Wild M-5 stereomicroscope and a Zeiss phase-contrast microscope. Drawings were made with the assistance of a camera lucida. Types of slide mounts made for study included temporary mounts in glycerol as well as permanent mounts stained with one of the following methods: fast green with lactic acid, chlorazol black, lignin pink in polyvinyl acetate, methylene blue with lactic acid, or silver nitrate and Dektol.

Ultrastructural morphology was studied using three types of scanning electron microscopes: ISI SuperMini, Cambridge S-100 Stereoscan, and Cambridge S4-10. Specimens were prepared for electron microscopy using standard techniques (Felgenhauer, 1987).

Terminology used in this study is consistent with that of current literature on the Corallanidae (e.g. Delaney and Brusca, 1985; Bruce et al., 1982).

### HISTORICAL REVIEW OF CORALLANID TAXONOMY

The history of the Corallanidae is a tangled one, with considerable taxonomic and nomenclatural activity having taken place. The family was proposed by Hansen in 1890, along with the family Alcironidae. The latter family was placed in synonymy with Corallanidae (by Stebbing, 1904b), as was the family Argathonidae (by Hale, 1925). Various genera have been removed from the Corallanidae and used to erect new families: *Barybrotes* was used to establish the Barybrotidae by Hansen (1890), but was later placed in synonymy with the Aegidae of Dana, 1853, by Pillai (1967); *Tridentella* was removed to the family Tridentellidae by Bruce (1984); *Excorallana* was removed to the Excorallanidae by Stebbing (1904a), but was returned to the Corallanidae by Bruce et al. (1982). Bruce et al. (1982) discussed the status of the Corallanidae and considered it to contain eight valid genera. As mentioned above, one of these (*Tridentella* Richardson, 1905) was subsequently removed to a new family; another, *Austroargathona* Riek, 1953, is herein placed in junior synonymy with the genus *Tachaea*. Delaney and Brusca (1985) discussed the status of the Tridentellidae and provided a key to the genera of the Corallanidae and Tridentellidae. Because the Corallanidae resembles four other flabelliferan families, a key to these five very similar families is provided below.

### KEY TO THE FLABELLIFERAN FAMILIES CYMOTHOIDAE, AEGIDAE, CIROLANIDAE, TRIDENTELLIDAE, AND CORALLANIDAE

1) Pereopods 4–7 prehensile (dactyli longer than propodi and markedly curved); antenna reduced, without clear distinction between peduncle and flagellum; maxillipedal palp 2-articulate ........................ Cymothoidae
– Pereopods 4–7 ambulatory (dactyli shorter than propodi and not markedly curved); antenna not as above, with clear distinction between peduncle and flagellum; maxillipedal palp 2–5-articulate .................................. 2
2) Maxilliped and maxilla with stout, recurved apical spines; maxillule lateral lobe forms a slender stylet; maxillule medial lobe small, without stout circumplumose spines; mandible sometimes with molar process, usually without lacinia mobilis .................................. Aegidae
– Maxilliped and maxilla without stout, recurved apical spines; maxillule lateral lobe does not form a slender stylet; maxillule medial lobe with or without stout circumplumose spines; mandible with or without lacinia mobilis and molar process .................................. 3
3) Mandible with well-developed lacinia mobilis and large, spinose, bladelike molar process; maxilliped with endite; maxillule lateral lobe with 11–14 apical spines; maxillule medial lobe large, with 3–4 stout, circumplumose spines; maxilla biramous .............. Cirolanidae

- Mandible with lacinia mobilis absent, or weakly developed if present; molar process sparsely spined and small or moderately sized, or absent; maxilliped with or without endite; maxillule lateral lobe with 1–5 stout apical spines; maxillule medial lobe small, without 3–4 stout circumplumose spines; maxilla uniramous ....... 4

4) Mandible without lacinia mobilis; mandible with nonspinose, moderately sized molar process; maxilliped with endite, palp always 5-articulate; maxillule lateral lobe styliform, slightly curved, tapering to apex with 3–5 stout, hooklike spines and smaller subapical spines; maxilla stout, 2-articulate, conical apical article often with tridentate scalelike spines ....... Tridentellidae

- Mandible with lacinia mobilis absent, or with lacinia mobilis represented by small, feeble spine row; mandible molar process nonspinose, small or absent; maxilliped without endite, palp 3–5-articulate; maxillule lateral lobe falcate with 1–3 large hooklike apical spines and 0–3 smaller subapical spines; maxilla small, represented by 1–4-articulate lobe, apex either a simple rounded lobe, a bifid or trifid lobe, or a sublinear and elongate article; maxilla apex without tridentate, scalelike spines ............... Corallanidae

The following synonymy lists only those references that are directly pertinent to the taxonomic and nomenclatural history of the family.

## Corallanidae Hansen, 1890

Corallanidae Hansen, 1890:280, 311, 376; Stebbing, 1893:345, 1904a:13, 1904b:703, 1907:39; Richardson, 1905:156; Thielemann, 1910:19; Hale, 1925:160; Kussakin, 1979:222; Bruce et al., 1982:464; Delaney, 1984:1; Bruce, 1984:447; Delaney and Brusca, 1985:728.

Alcironidae Hansen, 1890:312, 390; Stebbing, 1893: 346, 1900:637; Richardson, 1901:519; Moore, 1902:170.

Argathonidae Stebbing, 1905:17, 1911:179; Richardson, 1910:9.

Excorallanidae Stebbing, 1904b:704; Thielemann, 1910:19; Menzies and Glynn, 1968:41; Delaney, 1982:273.

Exocorallanidae Richardson, 1905:138 (*lapsus calami*).

Corallaninae Nierstrasz, 1917:102, 1931:163; Hale, 1940:293; Menzies, 1962a:115.

*Non* Corallanidae: *Tridentella* Richardson, 1905 (now in Tridentellidae Bruce, 1984); and *Barybrotes* Schioedte and Meinert, 1879 (now in Aegidae Dana, 1853).

*Incertae cedis: Corilana erythraea* Kossman, 1880. This poorly defined genus and species was regarded as *genus et species inquirenda* by Monod (1933) and regarded as closest to *Lanocira* by Bruce et al. (1982).

**DIAGNOSIS.** Flabellifera with eyes well developed; dorsum often ornamented with setae, spines, tubercles, or carinae; sexual dimorphism in ornamentation common. Antennule peduncle 2- or 3-articulate, basal article sometimes expanded. Antenna peduncle 5-articulate, articles 4–5 elongate. Frontal lamina always flat. Mandible with incisor variously modified; lacinia mobilis and molar process reduced or absent. Maxillule lateral lobe with 1–2 large falcate apical spines, with 0–3 smaller subapical (accessory) spines in some genera; medial lobe with simple apex, devoid of spines, sparsely setose. Maxilla uniramous, reduced, 1–4-articulate; apex morphology various, devoid of spines, sparsely setose. Maxilliped without endite; palp slender, 3–5-articulate, without apical spines; various maxilliped articles elongate in different genera.

**ADDITIONAL DESCRIPTION.** Dorsum moderately arched. Pereonites II–VII with distinct coxae. Pleon of 5 free segments plus pleotelson. Antennule and antenna flagella distinct, multiarticulate. Frontal lamina sessile, narrow, sometimes minute or absent in *Corallana* species. Clypeus generally short, wide, may or may not encompass labrum. Labrum usually small, narrower than clypeus, covering distal part of mandible incisor in some genera. Mandible with narrow 1–3 dentate incisor; molar process absent or reduced to small fleshy lobe; palp 3-articulate, either the middle or proximal article may be longest. Maxilla various: 1- or 2-articulate, short, round lobe; or simple lobe with bi- or trilobed apex; or 3- or 4-articulate, with apical article sublinear and elongate. Pereopods I–III subprehensile or "grasping" (dactylus as long as or longer than propodus), occasionally ambulatory (dactylus shorter than propodus), spinose. Pereopods IV–VII longer, always ambulatory, spinose. Pleopods biramous, lamellar; coupling spines and plumose setae present on medial margin of pleopod peduncles 1–4; peduncle lateral margin with simple spine. Pleopod exopods broader and more setose than endopods. Endopod of pleopod 5 without plumose marginal setae; endopod of pleopods 2–4 without plumose marginal setae in some species of *Tachaea* and *Corallana*. Male pleopod 2 with rodlike appendix masculina arising from proximal medial margin of endopod. Uropods inserted at base of pleotelson, both rami unfused.

**TYPE GENUS.** *Corallana* Dana, 1853.

**REMARKS.** The Corallanidae is a relatively small flabelliferan family. Museum specimens of the group are somewhat uncommon, with a few notable exceptions such as the collections of the USNM, BMNH, and ZMUC. The current study, though not an exhaustive treatment of the family at the species level, attempts to clarify the limits of the genera and provide a cladistic/biogeographic hypothesis about the evolution of the family.

The Corallanidae superficially resembles four other flabelliferan families (Cymothoidae, Aegidae, Tridentellidae, and Cirolanidae). Useful field characters that help in distinguishing corallanids from the very similar cirolanids include the generally larger eyes of the former, the distinctly visible coxae (in dorsal view), and the often present heavy setosity or dorsal tuberculation. However, for accurate determinations the appendages (particularly those of the head) must be examined.

## CHARACTERS OF DIAGNOSTIC UTILITY

Most of the diagnostic characters used to distinguish genera within the Corallanidae are those of mouthpart morphology, along with others such as features of the pereopods, antennae, pleotelson, frontal lamina, and eyes. A discussion of these characters in relation to the closely related families Tridentellidae and Cirolanidae (both used as outgroups in the cladistic analysis) follows.

There is a trend towards reduction of the lateral (outer) lobe of the maxillule among these three families. The Cirolanidae have the lateral lobe of the maxillule with 10–14 apical spines, whereas in the Tridentellidae and Corallanidae the spines are reduced in number but increased in size. This trend culminates in a large single-spined (falcate) maxillule in the corallanid genera *Corallana, Excorallana, Lanocira,* and *Tachaea.*

The medial (inner) lobe of the maxillule likewise shows reduction, from the circumplumose spination in cirolanids to a simpler, nonsetose or sparsely setose lobe with simple apex in tridentellids and corallanids. In the corallanid genera *Alcirona* and *Argathona,* the medial lobe of the maxillule is sometimes distally expanded, with a truncate apex.

The maxillae of cirolanids usually have both medial and lateral lobes; tridentellids and corallanids have reduced, uniramous maxillae with several different types of apex morphology, the most derived being the small, 2–3-articulate rounded lobe seen in *Alcirona, Argathona, Tachaea,* and *Corallana.* In *Lanocira* the maxilla is 3–4-articulate, with a sublinear, elongate apical article. In *Excorallana* the maxilla is a simple lobe, 1–2-articulate, with a bi- or trilobed apex. Tridentellid maxillae are stout, with rounded/conical apices and often with dentate, scalelike apical spines.

Mandible morphology trends from the short, broad, generally tricuspid-incisored cirolanid mandible to a mandible with a more slender trunk and long, falcate incisor seen in *Excorallana* and some species of *Corallana* (whose species show both conditions of long- and short-incisored mandibles). The mandibular molar process is reduced from the more robust, saw-toothed blade of cirolanids to a smaller, spineless, more slender, blade-shaped or lobelike molar process in corallanids. The robustly spined lacinia mobilis of the Cirolanidae is reduced to a small, sparsely spined lobe in some corallanid genera or lost in others and in the Tridentellidae. The mandibles of *Lanocira* have a unique character of dentate processes or teeth behind the incisor region.

The maxillipeds of corallanids show various degrees of palp fusion, as in many other isopod families (see generic Remarks sections for detailed discussion of palp article fusion in *Argathona* and *Tachaea*). Cirolanids and tridentellids generally possess a 5-articulate palp, but *Argathona* and *Tachaea* exhibit palps that vary from 3- to 4- to 5-articulate. The most derived corallanid genera, *Tachaea, Excorallana,* and *Corallana,* have unique characters of maxilliped article size; elongate middle palp articles in *Excorallana,* and elongate maxilliped bases in *Tachaea* and *Corallana.* The large endite evident on cirolanid maxillipeds and retained in the Tridentellidae is lost in the Corallanidae.

The 3-articulate antennule peduncle of cirolanids and tridentellids shows varying degrees of reduction in the Corallanidae. In *Alcirona, Argathona, Lanocira,* and *Tachaea* it is 2-articulate but varies from 2- to 3-articulate in *Excorallana* and *Corallana.* The antennule peduncle is expanded in size in the most derived corallanid genera, *Tachaea, Excorallana,* and *Corallana,* compared to the antennule peduncles of cirolanids and tridentellids.

In contrast to the Cirolanidae, where many genera have frontal laminae that project antero- or posteroventrally, the frontal laminae of tridentellids and corallanids are always flat and "sessile." The most derived genus, *Corallana,* has some species with the frontal lamina either greatly reduced or absent altogether.

The pereopods of tridentellids and corallanids are usually quite spinose; some corallanid genera have unique pereopod characters, such as the medially produced carpi on the first pereopods of *Tachaea* species, and the serrate dactyli typical of many species of *Alcirona* and several of *Argathona* and *Lanocira.*

Two unique characters present in certain corallanids are the lateral pleotelson incisions found only in some *Excorallana* species and the unpigmented, transverse band bisecting the eyes of several *Argathona* species.

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The Corallanidae contains six genera, with 67 species as of this writing (Table 1). The family is confined mainly to tropical and subtropical shallow-water marine habitats, although *Tachaea* has been collected primarily from freshwater habitats, and *Corallana* has many species recorded from brackish water. Corallanids have been reported from depths of 287 m to the intertidal zone, as well as from freshwater lakes 362 m above sea-level (*Tachea*). Every genus contains species recorded from coral reefs, thus the family name is appropriate. A variety of substrate and habitat types has been reported for corallanids, including coral reefs, limestone conglomerate reefs, sandy beaches, basalt boulder reefs, mangroves, wood burrows, brackish areas, and freshwater. Corallanid species frequent cryptic habitats, and they are often found living on or in corals, calcareous sponges, ascidians, bryozoans, gorgonians, coralline algae, tubeworms, scypho-

**Table 1. Species list for the Corallanidae Hansen, 1890 (Flabellifera).**

- Genus *Alcirona* Hansen, 1890
  - *Alcirona indica* Nierstrasz, 1931
  - *Alcirona krebsii* Hansen, 1890 (type-species)
  - *Alcirona multidigita* (Dana, 1853)
  - *Alcirona niponia* Richardson, 1909
  - *Alcirona papuana* Nobili, 1905
- Genus *Argathona* Stebbing, 1905
  - *Argathona confine* Hale, 1925
  - *Argathona crenulata* Bruce, 1982
  - *Argathona japonica* Shiino, 1961
  - *Argathona macronema* (Bleeker, 1857)
  - *Argathona muraeneae* Bal and Joshi, 1959 (*genus inquirenda*)
  - *Argathona normani* Stebbing, 1905 (type-species)
  - *Argathona parca* Hale, 1940
  - *Argathona rhinoceros* (Bleeker, 1857)
  - *Argathona rostrata* Bruce, 1982
  - *Argathona setosa* Richardson, 1910
  - *Argathona stebbingi* Nierstrasz, 1931 (*genus inquirenda*)
  - *Argathona sulcata* Richardson, 1910
- Genus *Corallana* Dana, 1853
  - *Corallana africana* Barnard, 1914
  - *Corallana basalis* (Heller, 1868)
  - *Corallana bidentata* Jones, Icely, and Cragg, 1983
  - *Corallana brevipes* Schioedte and Meinert, 1879
  - *Corallana collaris* Schioedte and Meinert, 1879
  - *Corallana estuaria* Jones, Icely, and Cragg, 1983
  - *Corallana furcilla* Barnard, 1955
  - *Corallana glabra* Nierstrasz, 1931
  - *Corallana hirsuta* Schioedte and Meinert, 1879
  - *Corallana hirticauda* Dana, 1853
  - *Corallana kulai* Bruce, 1982
  - *Corallana leopoldi* (Nierstrasz, 1930)
  - *Corallana nodosa* Schioedte and Meinert, 1879
  - *Corallana sculpta* (Milne-Edwards, 1840)
  - *Corallana* sp. Bruce, 1982 (female only)
  - *Corallana tridentata* Jones, Icely, and Cragg, 1983
- Genus *Excorallana* Stebbing, 1904
  - *Excorallana acuticauda* (Miers, 1881)
  - *Excorallana angusta* Lemos de Castro, 1960
  - *Excorallana berbicensis* Boone, 1919
  - *Excorallana bruscai* Delaney, 1984
  - *Excorallana costata* Lemos de Castro, 1960
  - *Excorallana fissicauda* (Hansen, 1890)
  - *Excorallana houstoni* Delaney, 1984
  - *Excorallana longicornis* Lemos de Castro, 1960
  - *Excorallana meridionalis* Carvacho and Yanez, 1971
  - *Excorallana mexicana* Richardson, 1905
  - *Excorallana oculata* (Hansen, 1890)
  - *Excorallana quadricornis* (Hansen, 1890)
  - *Excorallana richardsonae* Lemos de Castro, 1960
  - *Excorallana sexticornis* (Richardson, 1901)
  - *Excorallana stebbingi* Lemos de Castro and Lima, 1976
  - *Excorallana subtilis* (Hansen, 1890)
  - *Excorallana tricornis occidentalis* Richardson, 1905

**Table 1. Continued.**

  - *Excorallana tricornis tricornis* (Hansen, 1890) (type-species)
  - *Excorallana truncata* (Richardson, 1899)
  - *Excorallana warmingii* (Hansen, 1890)
- Genus *Lanocira* Hansen, 1890
  - *Lanocira anasicula* Jones, 1982
  - *Lanocira gardineri* Stebbing, 1904
  - *Lanocira glabra* Jones, 1982
  - *Lanocira kroyeri* Hansen, 1890 (type-species)
  - *Lanocira latifrons* Stebbing, 1909
  - *Lanocira rapax* (Moore, 1902)
  - *Lanocira rotundicauda* Stebbing, 1904
  - *Lanocira zeylanica* Stebbing, 1905
- Genus *Tachaea* Schioedte and Meinert, 1879
  - *Tachaea caridophaga* Riek, 1953
  - *Tachaea chinensis* Thielemann, 1910
  - *Tachaea crassipes* Schioedte and Meinert, 1879 (type-species)
  - *Tachaea lacustris* Weber, 1892
  - *Tachaea picta* Riek, 1967
  - *Tachaea spongillicola* Stebbing, 1907

zoans, and tube-building snails. Corallanids emerge from these cryptic habitats and "commensal" associations to temporarily parasitize or prey on fish, rays, shrimp, and turtles, as well as to prey on microcrustaceans such as mysids (Guzman et al., 1988).

Various species in different genera have been reported from more than one habitat and/or host. The number of species within a genus that have been reported as temporary parasites of either fish, rays, turtles, or shrimps varies greatly as follows: *Tachaea*—84%, *Argathona*—50%, *Alcirona*—40%, *Excorallana*—25%, *Corallana*—20%, and *Lanocira*—13%.

Three of the genera, *Argathona, Corallana,* and *Tachaea,* are restricted to the Indo-West Pacific. *Excorallana* is generally restricted to tropical and subtropical regions of the New World (Delaney, 1984), with only one species found outside that range: *Excorallana oculata,* a Caribbean species, which has also been reported off West Africa. The two remaining genera, *Alcirona* and *Lanocira,* are circumtropical, both being most diverse in the Indo-West Pacific, with only two to three species in each genus occurring in the New World.

The predilection for temporary parasitism noted above may partly account for the presence of *Alcirona* in both the Old and New World tropics, as individuals may have dispersed via temporary association with fish (or other) "hosts." However, both *Argathona* and *Tachaea* have a high percentage of species recorded as temporary parasites (50% and 84%, respectively) and yet are restricted to the Indo-West Pacific region. *Tachaea* has the highest percentage of temporary parasitism in the family and is known almost exclusively from fresh-

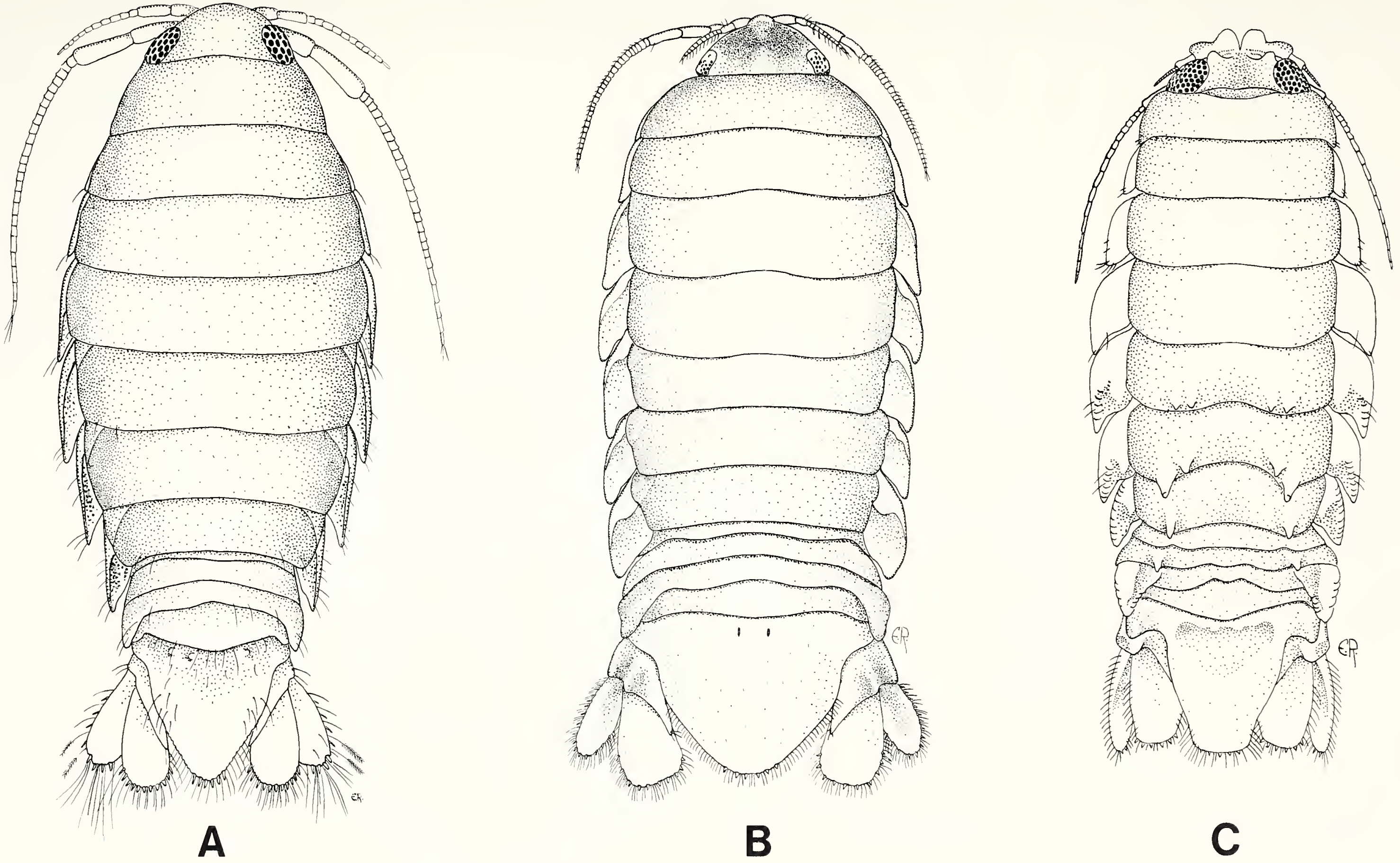


Figure 1A–C. Dorsal views: **A,** *Alcirona krebsii,* AHF male, length = 10 mm; **B,** *Argathona rhinoceros,* CAS 018845, male, length = 18.4 mm; **C,** *Corallana estuaria,* BMNH 1921.5.23: 80–82, male, length = 10 mm.

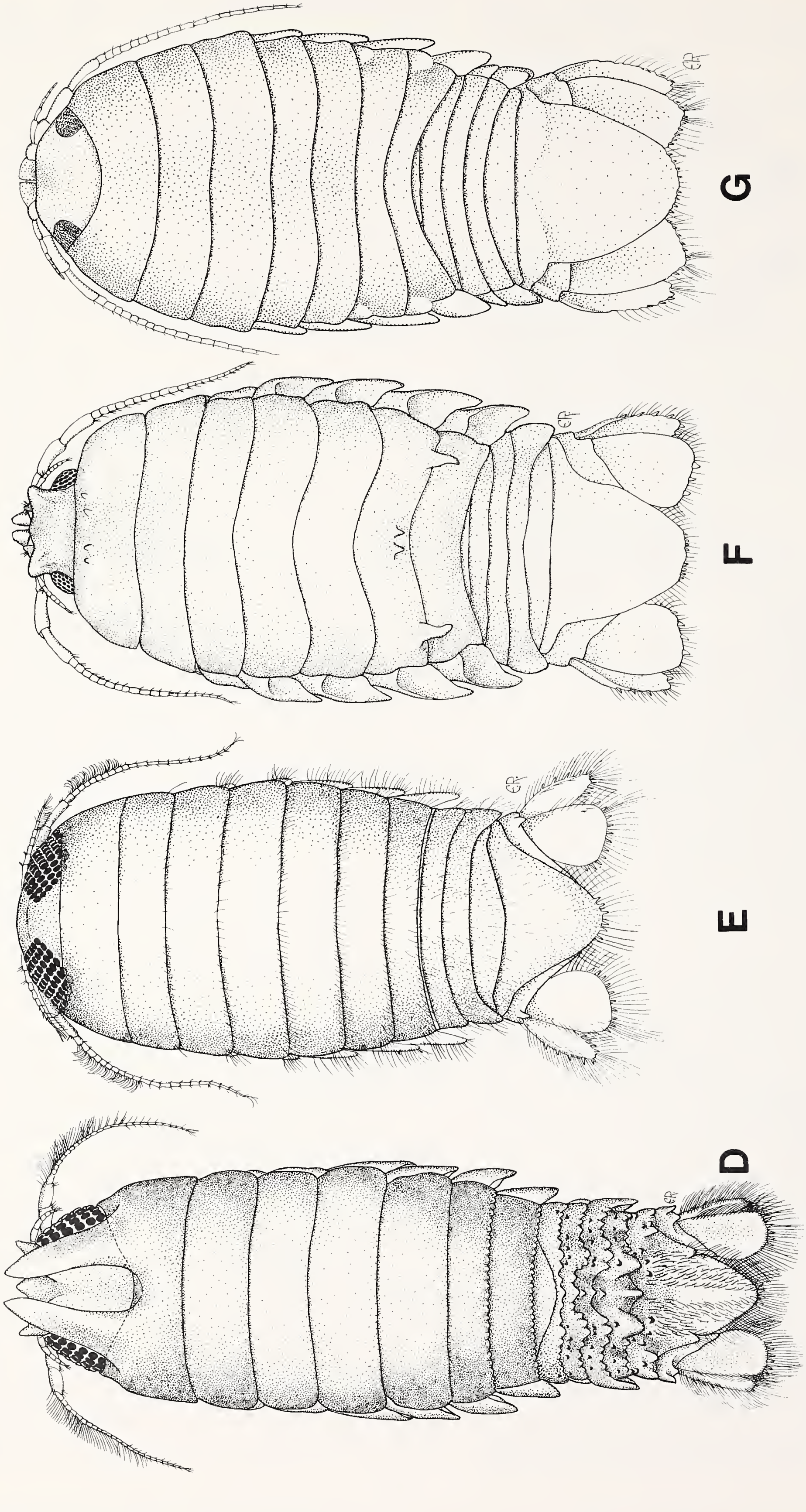


Figure 1D–G. Dorsal views: D, *Excorallana bruscai*, AHF 6611, male holotype, length = 7.88 mm; E, *Lanocira zeylanica*, AHF, male, length = 7.5 mm; F, *Tachaea lacustris*, ZML

water shrimp hosts; only one species is marine, collected from a coral reef. *Corallana* is also an Indo-West Pacific endemic, yet has only 20% of its species reported as temporary parasites. However, 40% of *Corallana* species are reported from wood burrows, in estuarine or brackish-water habitats, indicating a slightly different ecological orientation.

There is only one record (this study) of a species of *Lanocira* being collected as a temporary parasite of a fish (*Variola louti,* family Serranidae). The genus has never been reported from rays, turtles, or shrimp. Besides the usual cryptic habitats of corals, sponges, ascidians, and tubeworms, *Lanocira* has also been collected from the umbrella of the scyphozoan *Cassiopea andromeda.* Dispersal via such "hosts" may be partly responsible for the presence of *Lanocira* in both the Old and New World tropics.

Only three genera are found in the New World: *Excorallana, Lanocira,* and *Alcirona. Excorallana* is the largest genus in the family and its species exploit a wide variety of hosts and habitats—temporary parasitism of fish and rays, and "commensal" associations with sponges, ascidians, gorgonians, bryozoans, tube-molluscs, corals, and mangroves. Many *Excorallana* species have been collected with night-lights, and one species (*E. tricornis occidentalis*) exhibits definite nocturnal mass-migrating behavior into the water column, perhaps preying on other microcrustaceans (Guzman et al., 1988). Menzies and Kruczynski (1983) presented evidence suggesting that some species of *Excorallana, Alcirona,* and *Lanocira* may partition their habitat by depth range. *Excorallana* is restricted almost exclusively to the New World (save one species, see above). *Lanocira* and *Alcirona* are represented by only two to three species in the New World. The relative paucity of species of other corallanid genera in the New World may have allowed *Excorallana* to radiate in a greater variety of ecological niches in this region.

## CLASSIFICATION OF THE GENERA

The following are recognized as valid genera in the Corallanidae:

Family Corallanidae Hansen, 1890
  Genus *Alcirona* Hansen, 1890
  Genus *Argathona* Stebbing, 1905
  Genus *Corallana* Dana, 1853
  Genus *Excorallana* Stebbing, 1904
  Genus *Lanocira* Hansen, 1890
  Genus *Tachaea* Schioedte and Meinert, 1879

A key to the genera of the Corallanidae follows; this key updates that of Delaney and Brusca (1985).

## KEY TO THE GENERA OF THE CORALLANIDAE

1) Maxilliped palp middle article elongate; maxilla apex bi- or trilobed; mandible with elongate, falcate incisor ................ *Excorallana*
- Maxilliped palp middle article not elongate; maxilla apex not as above; mandible not as above ........................................ 2
2) Maxillule lateral lobe a single large falcate spine; maxilla 3- or 4-articulate, apical article sublinear, elongate; mandible with slender trunk and row of small spines behind incisor, mandible incisor not elongate .............. *Lanocira*
- Maxillule lateral lobe not a single large falcate spine; maxilla a short, rounded lobe; mandible not as above ......................... 3
3) Maxillule lateral lobe with 1 large falcate spine and 1–4 small hooklike accessory spines; mandible trunk and apex wide, incisor well developed but not elongate or falcate; maxilliped palp 4- or 5-articulate ............... *Argathona*
- Maxillule lateral lobe not as above; mandible trunk and apex narrow, incisor not elongate; maxilliped palp 3-, 4-, or 5-articulate ...... 4
4) Maxillule lateral lobe with 2 large falcate spines and 0–3 small accessory spines between the large ones; maxilliped palp always 5-articulate; maxilliped basis not elongate .......... *Alcirona*
- Maxillule lateral lobe with 1 large falcate spine and without small accessory spines; maxilliped palp 3-, 4-, or 5-articulate; maxilliped basis elongate .................................. 5
5) Maxilliped palp 3-, 4-, or 5-articulate; maxilliped basis length 1.5–2.0 times width; mandible with small, monocuspid incisor; inner angle of pereopod I carpus strongly produced; frontal lamina elongate, length 2.0–3.0 times width, quadrangular, rounded anteriorly, narrowing posteriorly ......................... *Tachaea*
- Maxilliped very narrow, palp always 5-articulate; maxilliped basis length 2.0–4.0 times width; mandible with bi- or tricuspid incisor; inner angle of pereopod I carpus not produced; frontal lamina not elongate, shape various, occasionally reduced or absent ............... *Corallana*

## Genus *Alcirona* Hansen, 1890

*Alcirona* Hansen, 1890:391; Stebbing, 1893:315, 1900:637, 1904b:708; Richardson, 1900a:217, 1901:519, 1902:277, 1905:156, 1909:78, 1910:8, 1914:361; Moore, 1902:170; Nobili, 1905:502; Nierstrasz, 1917:97, 1918:106, 1931:166; Hale, 1925:161; Monod, 1926:97; Nordenstam, 1946:10; Menzies and Glynn, 1968:43; Birkeland et al., 1976:159; Monod, 1975:1003, 1976:853; Bruce, 1982a:13; Bruce et al., 1982:464; Menzies and Kruczynski, 1983:67; Delaney and Brusca, 1985:728; Delaney, 1986:734.

## MATERIAL EXAMINED

*Alcirona krebsii:* 1) West Indies, ZMUC syntype, "coll. from *Pseudoscarus coeruleus,*" 1 fe., 16.4

mm; 2) West Indies, ZMUC syntype, "coll. from *Pseudoscarus psittacus,*" 1 fe., 6.4 mm; 3) West Indies, ZMUC syntype, "coll. from *Scarus* sp.," 1 spec. (pleon missing), 8.8 mm; 4) West Indies, ZMUC syntype, "coll. from *Pseudoscarus superbus,*" 1 fe., 8.4 mm; 5) West Indies, ZMUC syntype, "from *Priacanthus macrophthalmus,*" 1 fe., 14 mm; 6) West Indies, St. Thomas, 1 ma., 9.1 mm; 7) Florida, west coast, Pepperfish Key, USNM 44262, Sta. 7161, depth 14 m, 1 ma.; 8) no locality, USNM 20475, *Albatross,* Sta. 2365, 2 fe. and 1 ma.; 9) Panama, Panama Bay, USNM 66055, Smithsonian Biological Survey Sta. 139/465, 1 ma.; 10) Florida, Tortugas, USNM 39855, "from *M. venenosa,*" 1 fe.; 11) Florida, Hillsborough County, about 29 km west of Egmont Key, USNM 170828, R/V *Hernan Cortez* Sta. 67-328, 27°37′N, 83°07′W, depth 18 m, 26 spec.; 12) Costa Rica, Playas Blancas, USNM Acc. No. 131571, "from 2 lumps *Pavonia* coral, south shore of bay," 1 fe. and 1 ma.; 13) West Indies, USNM Acc. No. 208263, Sta. 106-56, 1 fe. (gravid); 14) Mexico, Baja California Sur, off Cabo San Lucas, USNM 39364, R/V *Albatross,* Sta. 2829, depth 56 m, 1 spec.; 15) Costa Rica, Cocos Island, Roca Sucia, "from grunge under rocks and coral," 1 fe.; 16) Indian Ocean, USNM IIOE Program, SOSC Acc. No. 23, *Anton Bruun* Cruise 4B, Sta. 269c, 7 fe. and 5 ma.; 17) (as *Alcirona insularis* holotype) Samoa, Mus Godeffroy, ZMUC, 1 fe., 4.1 mm; 18) Haiti, east coast, USNM 90445, coll. Johnson-Smithsonian Deep-Sea Expedition, Sta. 52/289, 19°10′5″N, 69°21′25″W, depth 25–40 m, 1 fe.; 19) Bahamas, USNM 119496, coll. Böhlke, Sta. 516, 1 ma.; 20) South Pacific Ocean, Tuvalu, Ellice Islands, Funafuti, USNM 46431, coll. 1899–1900 U.S. Fish Commission Expedition, Steamer *Albatross,* 1 spec.; 21) Panama, Panama City, San Francisco reef, USNM Acc. No. 144344, "Taken from eel *Echidna nocturna*"; 22) Panama, Miraflores Locks, coll. P.W. Glynn, 1 adult and 1 manca. *Alcirona niponia:* 1) Japan, Korea Strait, east channel off Oki Shima, USNM 039498 (type), coll. Bureau of Fisheries, Sta. 4879, depth 106 m, 1 ma. *Alcirona* spp.: 1) Colombia, Gorgona Island, AHF 412-35, coll. R/V *Velero,* "off coconut beach," 1 ma.; 2) Mexico, Sonora, Puerto Penasco, Gulf of California, University of Arizona No. 75-40, "Station beach reef poison station, water temp. 23–26 C.," 1 fe. (gravid); 3) Marquesas Islands, Fatu Hiva, west coast, USNM Acc. No. 291828, coll. Marquesas Expedition, Sta. FHI, Haul 2, "with broken shell, rubble and flat live coral," depth 67–72 m, 2 ma. and 4 fe.; 4) Panama, Farfan Point, 8°56′N, 79°34′W, "in sand/mud/rocks at low tide with an ichthyocide, depth 0–1.3 m," 6 spec.; 5) Colombia, Ensenada de Utria, Choco, "between dead coral," 2 fe., 9.5 and 11.4 mm, and 1 ma., 8.5 mm; 6) Panama, Isla Perlas, "from interstices of *Pocillopora,*" coll. P.W. Glynn, 4 spec.

## DIAGNOSIS

Antennule peduncle 2-articulate; basal article of peduncle narrow, not expanded. Frontal lamina narrow, pentagonal; clypeus large, crescent-shaped or subtriangular; labrum small, width twice length. Mandible with short incisor, molar process and lacinia small or absent. Maxillule lateral lobe apex with 2 large falcate spines, and 0–3 smaller spines between the large ones; medial lobe apex simple, blunt. Maxilla 2-articulate, rounded lobe. Maxilliped without endite; maxilliped basis not elongate; palp always 5-articulate, middle article not elongate. Anterior pereopods often with serrate dactyli and propodi; carpi not greatly produced on posteromedial margins as in *Tachaea.*

## ADDITIONAL DESCRIPTION

Corallanidae with eyes small, round, placed at posterolateral angles of cephalon. Body often with dorsal setae or tubercles (Fig. 1A). Postlateral angles of clypeus produced almost to articulation of mandibular palps (Fig. 2D). Mandible trunk and apex narrow, incisor short; molar process usually absent, but small molar process present in some species (Figs. 2A, B); lacinia mobilis absent (Figs. 2A–C, 3E, F). Palp inserted near mandible base, 3-articulate, middle article longest, middle and distal articles with simple and comb setae (Figs. 2A, C). Maxillule lateral (outer) lobe slender, tapering apically (Figs. 2G, 3C, D) and often with comblike cuticular structures on medial margin (Figs. 4B–D). Maxilla simple, with small setae on rounded apical article (Figs. 2F, 3B). Maxilliped palp apical article with plumose setae, groups of 1–3 setae on margins of other articles (Figs. 2E, 3A, 4A). Pereopods I–III prehensile, with simple setae and robust spines on posteromedial margins; dactyli and propodi of some species with digitiform processes (Fig. 5A). Pereopods IV–VII longer than I–III, ambulatory, with stout spines and simple setae on posteromedial margins (Figs. 5B, C). Pleopod peduncles broader than long, with 3–5 coupling spines and group of proximal plumose setae on medial margins, lateral margins with 1 simple spine (Figs. 5D–H). Exopod of pleopods broader, longer, and with more plumose marginal setae than endopod. Endopod of pleopod 5 naked, proximal medial margin produced, lobelike (Fig. 5H). Male pleopod 2 with rodlike appendix masculina, with simple apex, arising from proximal medial margin of endopod (Fig. 5E).

## TYPE SPECIES

*Alcirona krebsii* Hansen, 1890:391, plate VIII, figures 1a–q, by designation (Menzies and Kruczynski, 1983).

## DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

1) *Alcirona multidigita* (Dana, 1853):768, figures 3a–f, plate 51. *Alcirona multidigitata* Stebbing, 1900:637; Nierstrasz, 1917:102, 1931:168; Monod, 1926:99 (*lapsus calami*).
*Aega multidigita* Dana, 1853:768.

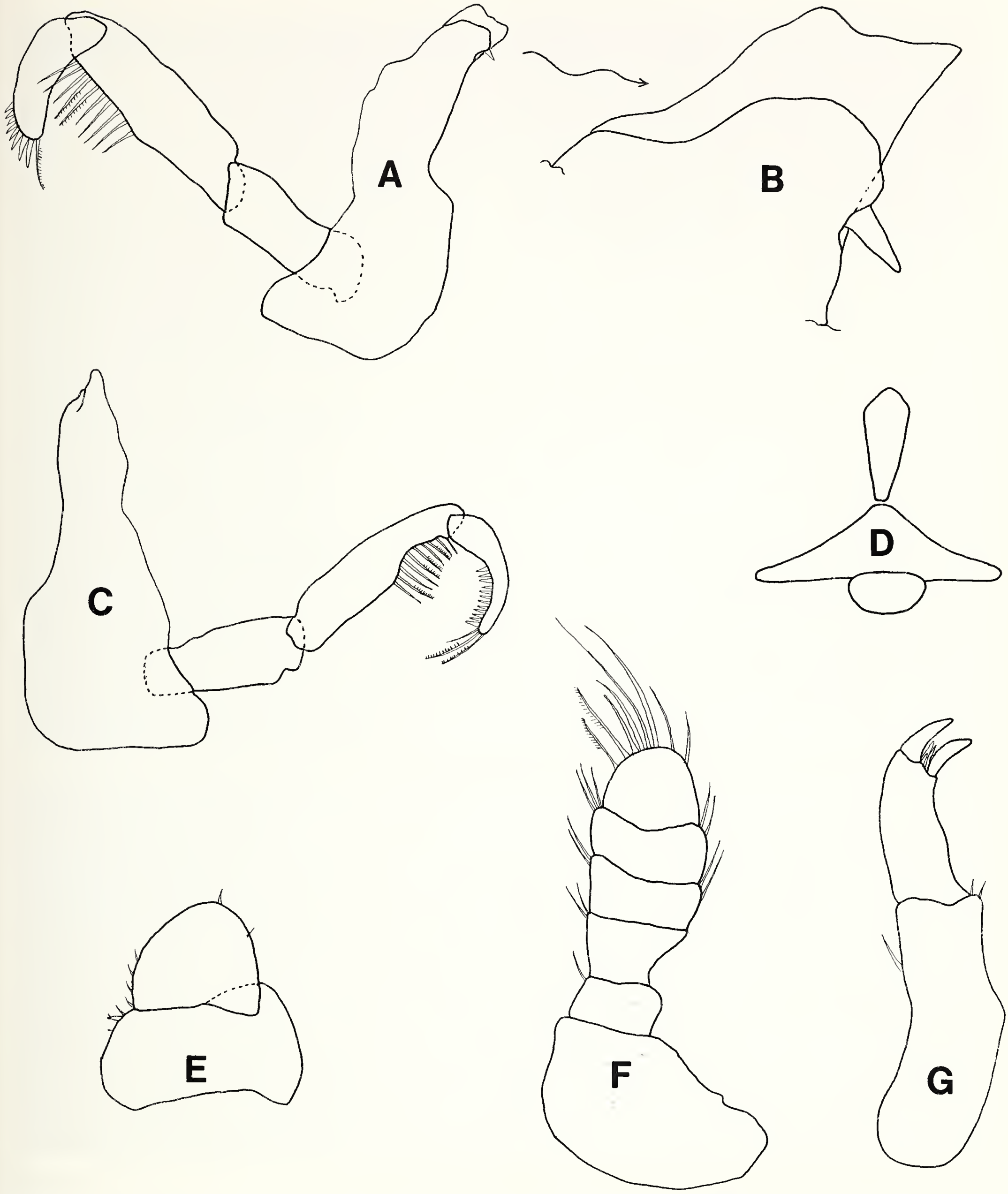


**Figure 2.** *Alcirona* sp., LACM specimen: **A,** left mandible; **B,** apex of left mandible; **C,** right mandible; **D,** frontal lamina, clypeus, and labrum; **E,** maxilliped; **F,** maxilla; and **G,** maxillule.

*Cirolana multidigitata* Miers, 1878:511, 1884: 301 (*lapsus calami*).

**DISTRIBUTION.** North Borneo; West Australia; and Zebu, Philippines.

2) *Alcirona krebsii* Hansen, 1890:391, figures 1a–q, table VIII. For synonymy see Menzies and Kruczynski, 1983:69.

**DISTRIBUTION.** Apparently a circumtropical species from collection records, but possibly a complex of sibling species. Localities for the synonyms listed above include Maldive Islands, Ellice Islands, Fiji Islands, Gulf of Mexico, Caribbean Sea, Bermudas, Marquesas Islands, Senegal, Samoa, New Britain, Papua New Guinea, Pacific Panama, Pacific Costa Rica, Baja California, Puerto Rico, and Bahamas.

3) *Alcirona papuana* Nobili, 1905:502, figures 5a–h, plate XIII. Nierstrasz, 1917:102, 1931: 169; Nordenstam, 1946:10.

**DISTRIBUTION.** Dutch New Guinea.

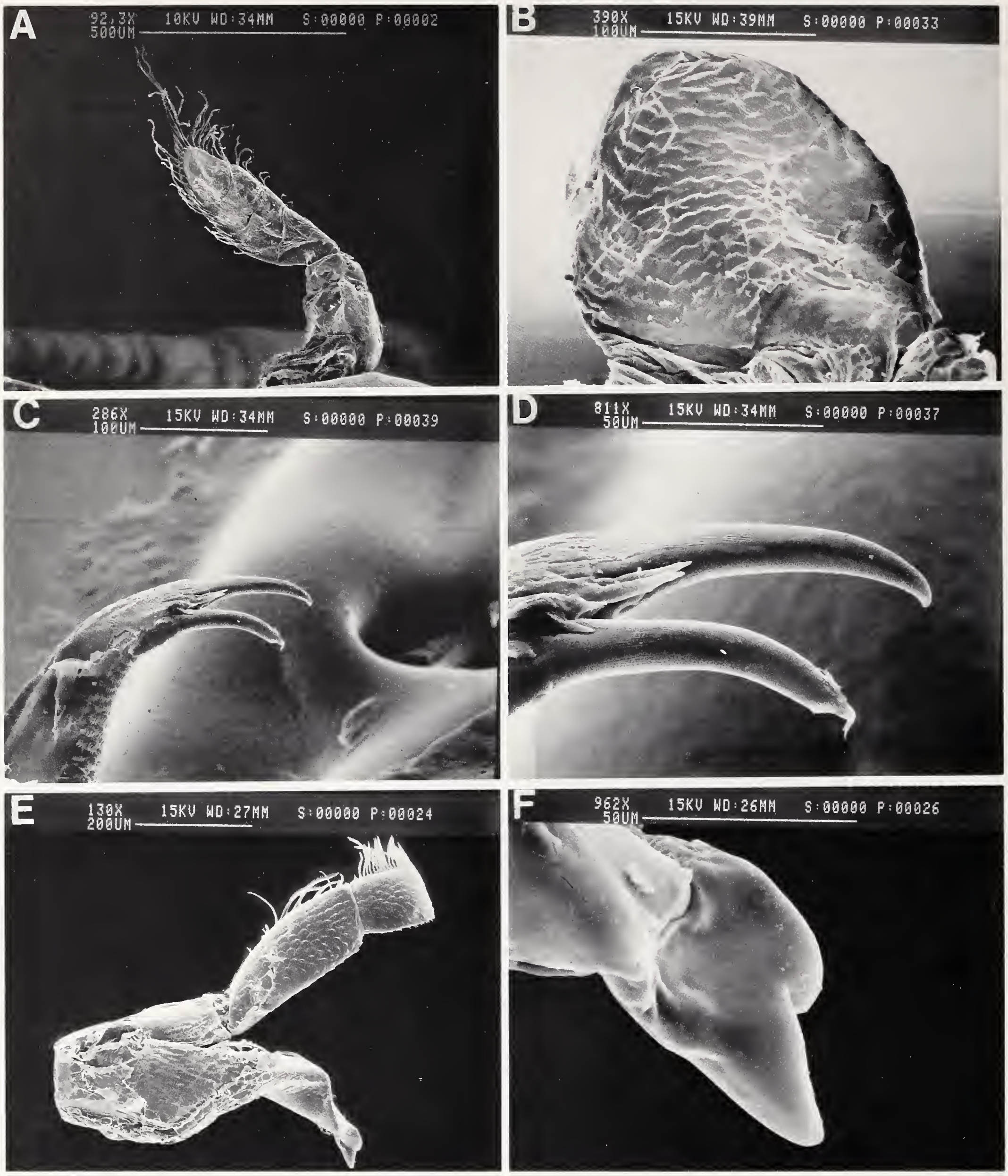

A
92.3X 10KV WD:34MM S:00000 P:00002
500UM
B
390X 15KV WD:39MM S:00000 P:00033
100UM
C
286X 15KV WD:34MM S:00000 P:00039
100UM
D
811X 15KV WD:34MM S:00000 P:00037
50UM
E
130X 15KV WD:27MM S:00000 P:00024
200UM
F
962X 15KV WD:26MM S:00000 P:00026
50UM

**Figure 3.** Scanning electron micrographs of *Alcirona krebsii:* **A,** maxilliped; **B,** maxilla; **C,** maxillule; **D,** maxillule apex; **E,** mandible; and **F,** mandible incisor.

4) *Alcirona niponia* Richardson, 1909:78, figure 6; Nierstrasz, 1917:102, 1931:167; Monod, 1926: 99.

**DISTRIBUTION.** Korea Strait, near Oki Shima.

5) *Alcirona indica* Nierstrasz, 1931:166, figures 38–45.

**DISTRIBUTION.** Dutch East Indies.

Non-*Alcirona: Alcirona pearsoni* Monod, 1926 (now *Argathona rhinoceros*); *Alcirona macronema* (Bleeker, 1857) (now *Argathona macronema*); and *Alcirona tuberculata* Richardson, 1910 (now *Cirolana tuberculata*).

## REMARKS

In 1890 H.J. Hansen proposed a new family, Alcironidae, for his new genera *Alcirona* Hansen, 1890; *Lanocira* Hansen, 1890; and *Tachaea* Schioedte and Meinert, 1879. The validity of Alcironidae was upheld by subsequent workers (Stebbing, 1893; Richardson, 1901; Moore, 1902) until Stebbing

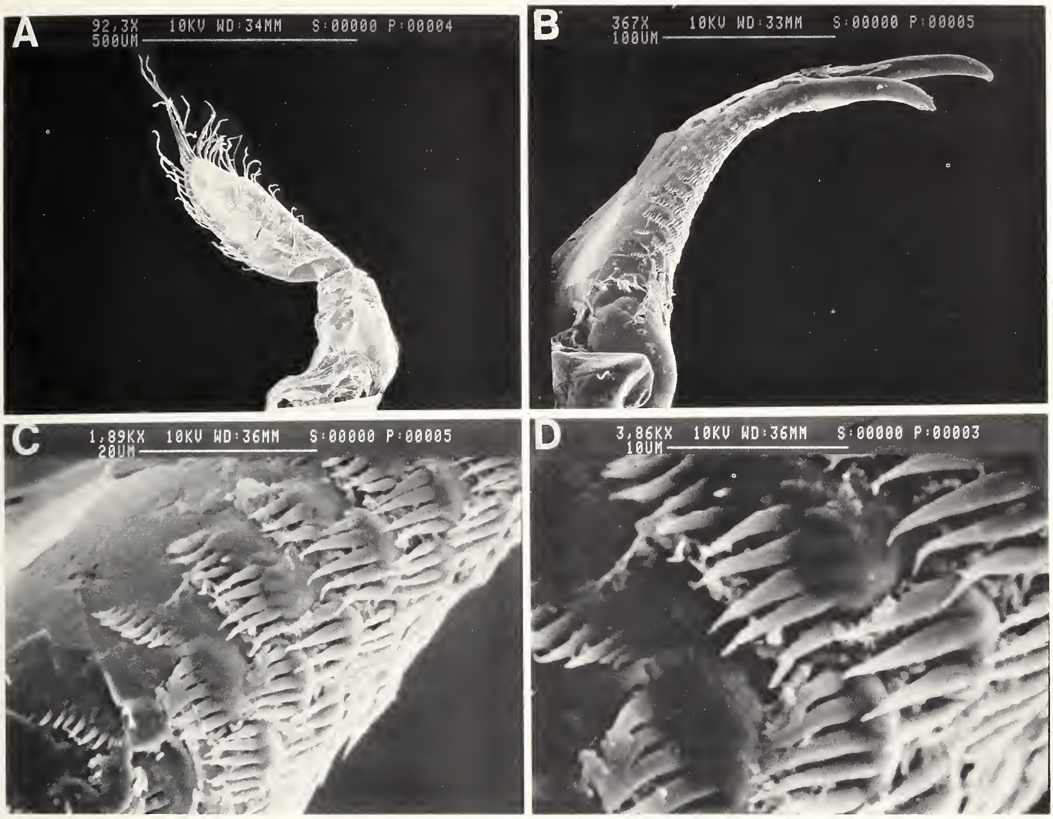

A
92,3X 10KV WD:34MM S:00000 P:00004
500UM
B
367X 10KV WD:33MM S:00000 P:00005
100UM
C
1,89KX 10KV WD:36MM S:00000 P:00005
20UM
D
3,86KX 10KV WD:36MM S:00000 P:00003
10UM

**Figure 4.** Scanning electron micrographs of *Alcirona krebsii:* **A,** maxilliped; **B,** medial margin of maxillule; **C,** cuticular structures on maxillule (detail of B); and **D,** detail of cuticular structures.

(1904b) concluded that the alcironid genera (*Alcirona, Lanocira,* and *Tachaea*), as well as *Corallana* Dana, 1853, should be placed in the Corallanidae.

With five species, *Alcirona* is the smallest genus in the Corallanidae. Menzies and Kruczynski (1983) recently synonymized *Alcirona insularis, A. hirsuta,* and *A. maldivensis* with *A. krebsii.* Some sexual variation is evident in the pleonal tuberculation, pereonal and pleonal setation, and dactyli serration of pereopods I–II in *Alcirona krebsii;* usually females have tuberculation, setation, and serration either reduced or absent (see Stebbing, 1900: 638; Nordenstam, 1946:12; Menzies and Glynn, 1968:43). According to Nordenstam (1946:12) and Menzies and Kruczynski (1983:69) variation in setosity and dactyli serration is also known to occur in males, and this led the latter authors, following Nordenstam's suggestion, to synonymize *A. hirsuta, A. insularis,* and *A. maldivensis* with *A. krebsii.* The five species of *Alcirona* are very similar to one another; given the sexual dimorphism in dactyli and propodi serration, and the amount of variation in the characters of setosity, tuberculation, and pleotelson shape within *A. krebsii,* females should be identified with care.

*Alcirona* is morphologically similar to *Argathona,* the major differences being the shape of the mandibles, the two large falcate spines on the apex of the lateral lobe of the maxillule, and the serrate dactyli of the anterior pereopods in *Alcirona* (the latter feature also has been reported in *Lanocira zeylanica* by Monod, 1933:184). Several species originally placed in *Alcirona* have been removed to *Argathona* (*Argathona macronema* and *Argathona rhinoceros*) by various authors. Bruce (1982a) suggested that *Argathona stebbingi* Nierstrasz, 1931, and *Argathona muraeneae* Bal and Joshi, 1959, may belong to the genus *Alcirona,* based on the figures of the maxillules and pereopods published for those species. The types of *A. stebbingi* and *A. muraeneae* have yet to be reexamined. Delaney (1986) removed *Alcirona tuberculata* Richardson, 1910, to the genus *Cirolana* based on features of mouth appendages.

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

All described *Alcirona* species except *A. krebsii* are found only in tropical/subtropical marine habitats in the Indo-West Pacific (Fig. 6). *Alcirona krebsii* is apparently a circumtropical species, occurring in the Pacific, Indian, and Atlantic Oceans.

Two *Alcirona* species have been collected as

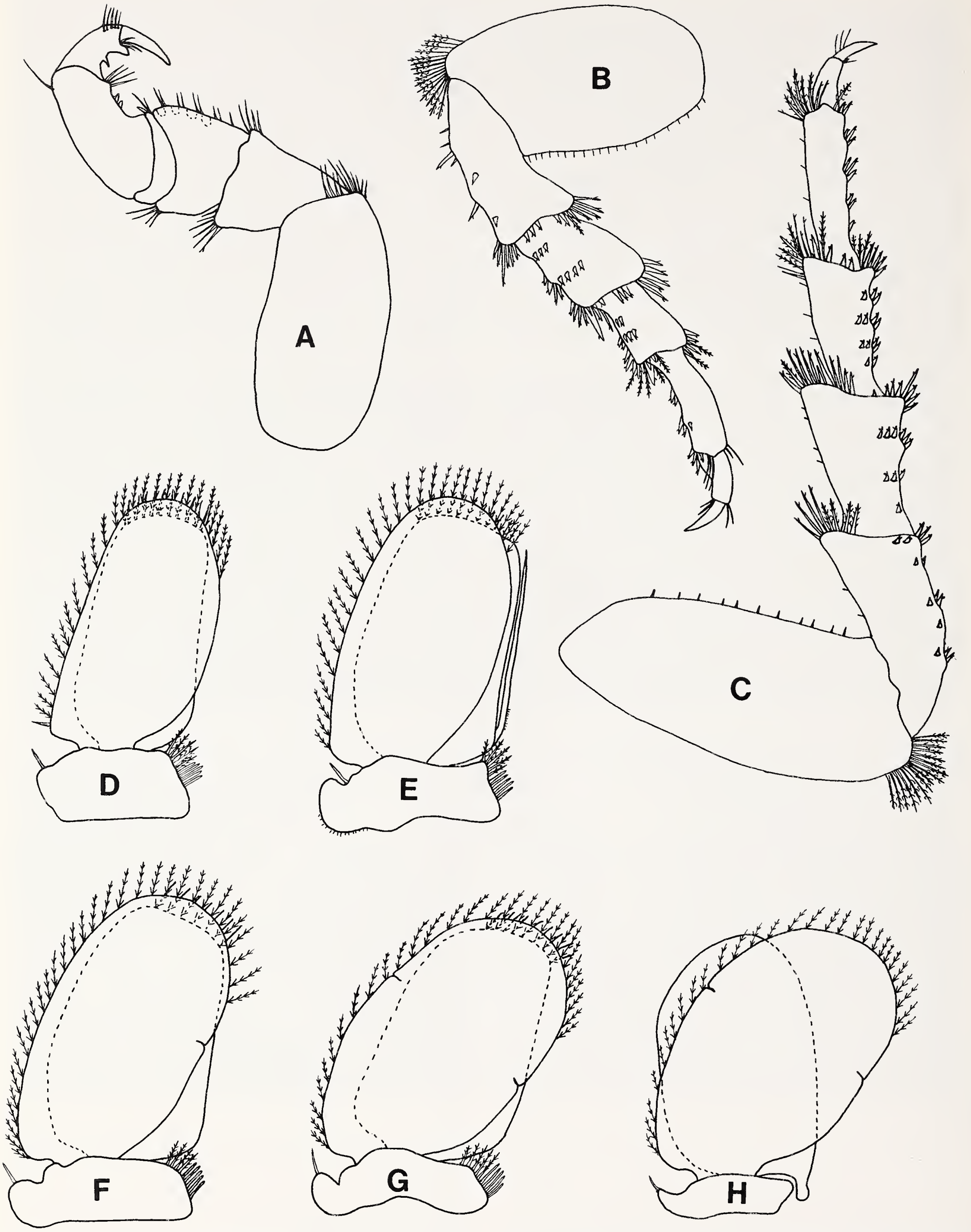


**Figure 5.** *Alcirona* sp., LACM specimen (Colombia): **A,** pereopod I; **B,** pereopod IV; **C,** pereopod VII; **D,** pleopod 1; **E,** pleopod 2; **F,** pleopod 3; **G,** pleopod 4; and **H,** pleopod 5.

"parasites": *A. krebsii* (from "fins of Hamlet Grouper," from fish "*M. venenosa*," *Pseudoscarus coeruleus, Pseudoscarus psittacus, Pseudoscarus superbus, Priacanthus macrophthalmus, Scarus* sp., and the eel *Echidna nocturna*) and *A. indica* (from *Amphacanthus* (*Teuthis*) *hexagonalus*). Other *Alcirona* species have been collected from a variety of substrates, including andesite rock, "*Pavonia* coral," coral reef rock, and fine gray sand/broken shell. *Alcirona krebsii* has been reported as a "commensal" from "living bathing sponges" (Hansen, 1890), and *A. multidigita* has been reported as a "commensal" from *Euplectella* or *Meyerina claviformis* (by Miers, 1878). *Alcirona* species have been

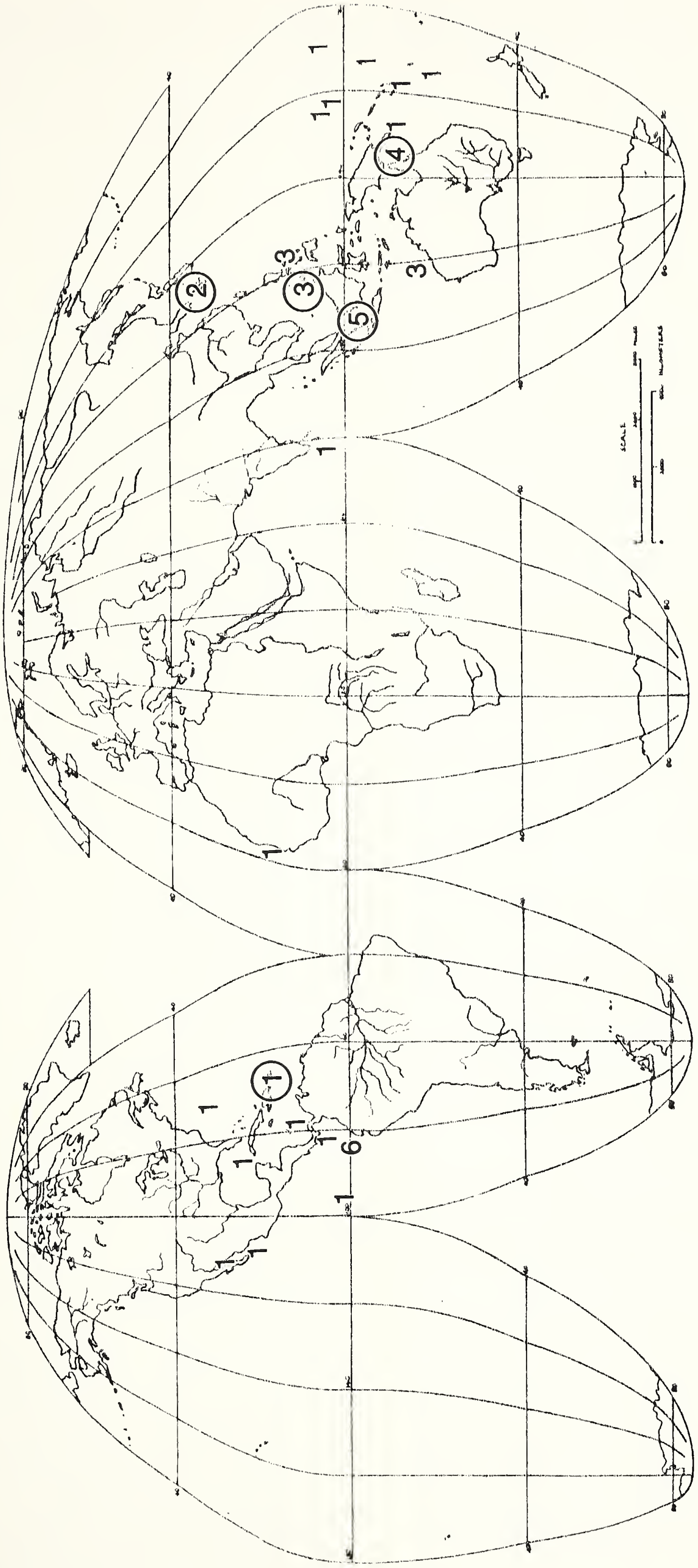


Figure 6. Distribution of *Alcirona* species; type localities are circled. Species numbers are: 1, *A. krebsii;* 2, *A. niponia;* 3, *A. multidigita;* 4, *A. papuana;* 5, *A. indica;* and 6, *A.* sp.

collected at depths ranging from the intertidal zone to 106 m. Menzies and Kruczynski (1983), conducting trawling operations in the Gulf of Mexico over a three year period, found *Alcirona krebsii* predominately at 18 m depth.

## Genus *Argathona* Stebbing, 1905

*Argathona* Stebbing, 1905:17, 1910:100, 1911:179; Richardson, 1910:9; Nierstrasz, 1917:102, 1931: 172; Hale, 1925:161, 1929:251, 1940:293; Monod, 1933:162, 161, 1929:251, 1940:293; Monod, 1933:162, 1975:999, 1976:853; Barnard, 1936: 154, 1940:500; Nordenstam, 1946:1; Bal and Joshi, 1959:563; Shiino, 1961:93; Pillai, 1967:272; Trilles and Paperna, 1980:445; Bruce, 1982a:12; Bruce, Brusca, and Delaney, 1982:464; Delaney and Brusca, 1985:728.

*Brotherus* Budde-Lund, 1908:306; Stebbing, 1911: 179; Nierstrasz, 1917:102; Hale, 1925:161; Monod, 1933:162, 1975:999.

*Gurida* Budde-Lund, 1908:305; Nierstrasz, 1917: 102, 1931:176; Monod, 1933:162, 1975:999.

*Orcilana* Nierstrasz, 1931:170; Monod, 1933:162, 1975:999.

### MATERIAL EXAMINED

*Argathona normani:* 1) Indian Ocean, USNM IIOE Program, SOSC Ref. No. 23, Sta. 206A, coll. International Indian Ocean Expedition, R/V *Anton Bruun* Cruise 4B, 20°23′N, 70°00′E, depth 73 m, 2 fe.; 2) Persian Gulf, Jaraid Island, USNM 101915, from shallow reef with *Aega basalis,* 1 fe.; 3) Australia, USNM Acc. No. 275759, BPI 13, 1 spec. *Argathona macronema:* (as syntype of *Corallana macronema*) Malaysia, BMNH 1880:6, coll. Bleeker, 1 fe., 15.4 mm. *Argathona rostrata:* 1) Papua New Guinea, Bootless Bay, Motapore Island, AM No. P32349, 09°31′S, 147°17′E, from sponge, 1 ma., 7.4 mm. *Argathona setosa:* 1) Philippine Islands, off Linao Point, USNM No. 40911 (holotype), R/V *Albatross,* Sta. 5254, depth 38 m, 1 fe. (gravid), 10.2 mm. *Argathona sulcata:* 1) Philippine Islands, Luzon, east coast, USNM No. 41010 (holotype), depth 263 m, coll. R/V *Albatross,* Sta. 5453, 1 fe., 19.5 mm. *Argathona macronema:* 1) Australia, AM No. P28791, LI-61, 1 fe., 11.6 mm, and 4 ma., 4.8, 4.9, 10, and 10 mm; 2) Seychelle Islands, ZMHUB No. 15732, 1 fe., 12.4 mm; 3) Taiwan, Takao, ZMHUB No. 14782, 1 ma., 15 mm; 4) Indian Ocean, Amirantes Islands, African Islands, off north end of north island, USNM Acc. No. 276969, depth 8–10 m, International Indian Ocean Expedition, Sta. F-78, 1 fe.; 5) Philippine Islands, Batananan Island, USNM No. 101935, 1 fe. (gravid); 6) Ponape, USNM Acc. No. 339879, UGS 80-2, 05°51′N, 158°20′E, depth 2 m, "with rotenone," 1 fe.; 7) Saudi Arabia, Red Sea, Jidda, SAMS Pier, USNM Acc. No. 17832, U-48-121, 2 fe.; 8) Seychelle Islands, Faon Island, off south shore of island, USNM Acc. No. 276969, depth 11–15 m, International Indian Ocean Expedition, Sta. F-11, 1 fe.; 9) Philippine Islands, Luzon, near Palag Bay, USNM No. 101936, 1 fe.; 10) Australia, Northern Territory, Cobourg Peninsula, Caiman Ck., USNM, "in mangrove, from nares of *Lutjanus argentimaculata,*" 3 juveniles; 11) Australia, Northern Territory, Cobourg Peninsula, Table Point, USNM, "from *Plectropoma maculata,*" 2 fe. and 13 juveniles; 12) Australia, Northern Territory, Cobourg Peninsula, Coral Bay, USNM, SM CP/62, 2 fe.; 13) (as *Argathona similis,* holotype) Indian Ocean, Indonesia, Celebes, Limbe Strait, USNM No. 41015, 1 fe., 16.5 mm; 14) Red Sea, Ethiopia, Heart Island, Sheikh el Abu, off lighthouse just west of south end of island, USNM Acc. No. 284009, Sta. VGS 69-14, 16°08′N, 39°26.5′E, depth to 4 m, "rotenone and dip net," 1 fe.; 15) Australia, Queensland, Capricorn Group, One Tree Island, lagoon, AM No. P28795, low tide, FT 106, 1 fe., 5.3 mm, and 1 manca, 3.2 mm; 16) Australia, Queensland, Capricorn Group, One Tree Island, AM No. P28794, depth 20–23 m, "from nostrils of *Plectropoma leopardus,*" FT 431, 1 fe., 14.7 mm, and 2 ma., 12.2 and 9.6 mm; 17) Israel, Gulf of Aqaba, northwest coast, about 1 mile north of Ras Burga, USNM Acc. No. 284009, Sta. VGS 69-6, depth to 8 m, "rotenone," 2 fe., 18 and 9 mm, and 1 ma., 8 mm; 18) Celebes, Limbe Strait, USNM, 1 fe., 15 mm. *Argathona rhinoceros:* 1) Thailand, Sattahip, Ko-I-Lao, CAS No. 018845, depth 1–3 m, Quad. #S-102720, 1 fe., 21 mm, 1 ma., 18.4 mm, and 3 mancas, 4.4, 4.8, and 5.2 mm; 2) Australia, Northern Territory, Cobourg Peninsula, Table Point, USNM, "from fish *Epinephilus malabaricus,*" 5 fe.; 3) Persian Gulf, Jaraid Island, USNM 101916, 27°20′N, 49°49′E, near Sta. 8, "from nasal opening of *Epinephalus taurina,*" 1 fe. and 3 ma.; 4) India, west of Cochin, USNM Acc. No. 280815, depth 90 m, "taken as parasite from nares of *Epinephelus chlorostigma,*" 7 fe. and 5 ma.; 5) Australia, Northern Territory, Cobourg Peninsula, Coral Bay, USNM, 16 May 1983, CP/60, "from nares of *Epinephalus malabaricus,*" 2 fe.; 6) Australia, Northern Territory, Cobourg Peninsula, Table Point, USNM, "from fish *Epinephelus malabaricus,*" 4 fe., 5, 10, 10, and 13 mm; 7) Indian Ocean, USNM Acc. No. 27085, coll. W.L. Abbott, 2 fe., 23 and 27 mm, and 1 ma., 21 mm; 8) Indian Ocean, Mozambique Channel, USNM IIOE Program, SOSC, R/V *Anton Bruun* Cruise 8, Sta. 408-F, 16°21′S, 43°59′E, depth 27 m, poison station, 2 fe., 20 and 8.2 mm; 9) West Pacific Ocean, Eniwetok Atoll, Parry Island, USNM Acc. No. 228273, "from ventral apex of right gill cavity of serranid *Variola louti* with *Lanocira* sp. and juvenile cymothoid," 1 fe.; 10) Indian Ocean, between Mozambique and Madagascar, USNM IIOE Program, SOSC, R/V *Anton Bruun* Cruise 8, Sta. 407-k, 15°52′S, 44°23′E, depth 30 m, "shrimp trawl," 3 fe. and 1 ma.; Palau Islands, Rattakadokoru Island, USNM 99286–99288, Sta. 97, 07°17′N, 134°15′E, "from outer edge of outer reef, west of island, in gill cavities and nares of fish *Plectropomus leopardis,*" 1 fe. and 2 ma. *Argathona con-*

*fine:* 1) Australia, Pt. Cairns, Alexander Reef, AM No. P31711, "from blue-spotted lagoon ray," 1 fe., 16 mm; 2) Australia, Northern Territory, Gulf of Carpentaria, reef at Yirrkala, northwest of Cape Arnhem, USNM 101918, coll. Arnhem Land Expedition, 7 spec.; 3) Australia, northwest of Cape Arnhem, from Ironstone Reef at Yirrkala, USNM 102146, "killed with 5% emulsified Rotenone," M48-21, 1 ma.; 4) Australia, northwest of Cape Arnhem, from coral reefs at Yirrkala, USNM 102147, M48-21, 16 spec. *Argathona* spp.: 1) Australia, Northern Territory, Cobourg Peninsula, USNM, CP/60/BCR, 1 fe., 16 mm, and 13 mancas; 2) Seychelle Islands, Anonyme Island, USNM Acc. No. 276969, International Indian Ocean Expedition, Sta. F-21, depth 0–2 m, "large sandy-bottom tidepool on east end of island," 1 manca; 3) Seychelle Islands, Anonyme Island, vicinity of Mahe, USNM Acc. No. 276969, IIOE, Sta. F-17, depth 0–3 m, 3 mancas; 4) Indian Ocean, Mozambique Channel, USNM, IIOE, Sta. 408-F, 16°21′S, 43°59′E, depth 27 m, coll. SOSC, R/V *Anton Bruun* Cruise 8, 1 fe., 9.5 mm; 5) Seychelle Islands, Beacon Island, off Port Victoria, USNM Acc. No. 276969, IIOE, Sta. F-26, depth 13–18 m, 1 ma.; 6) Indian Ocean, Admirantes Islands, D'Arros Island, off east side, USNM Acc. No. 276969, depth 18–30 m, 1 ma.

## DIAGNOSIS

Antennule peduncle 2-articulate; basal article of peduncle not expanded. Frontal lamina flat, narrow, and pentagonal; clypeus large, crescent, or inverted V-shaped, encompassing small labrum. Mandible trunk and apex wide; incisor well developed but not long as in *Excorallana*, mono- or bicuspid; molar process small, lacinia mobilis absent. Maxillule lateral lobe apex with 1 large falcate spine, and 1–4 small hooklike accessory spines at base of large spine; medial lobe simple, with widened, truncate apex. Maxilla short, 2- or 3-articulate lobe with broadly rounded apex. Maxilliped without endite; maxilliped basis not elongate; with broad, 4- or 5-articulate palp, middle article not elongate. Anterior pereopods usually without serrate dactyli (but present in *A. muraeneae* and *A. stebbingi*); carpi not greatly produced on posteromedial margins as in *Tachaea.*

## ADDITIONAL DESCRIPTION

Eyes well developed, at lateral margins of cephalon; in some species each eye bisected by transverse unpigmented band. Body occasionally with dorsal tubercles and setae; cephalon of some species with prominent, upwardly produced rostrum (Figs. 1B, 7I). Antennule basal article not expanded (Fig. 7H). Antenna peduncle articles 4–5 much longer than 1–3 (Fig. 7G). Frontal lamina, clypeus, and labrum visible anterior to mandibles; posterolateral angles of clypeus nearly reaching origin of mandibular palp (Fig. 7C). Mandible incisor short, well developed, mono- or bicuspid; palp inserted near mandible base, 3-articulate, middle article longest and with plumose marginal setae; distal article with simple or plumose marginal setae and often with comblike cuticular structures (Figs. 7F, 8C, E, F). Maxillule lateral lobe with comblike cuticular structures on medial margin; medial (inner) lobe with 0–3 spines on medial margin (Figs. 7B, 8D). Maxilla with 1–2 apical simple setae (Figs. 7D, E, 8B). Maxilliped palp distal articles with simple or plumose marginal setae (Figs. 7A, 8A). Pereopods I–III short, subprehensile, with simple setae and robust spines on posteromedial margins (Figs. 9A, D). Pereopods IV–VIII longer, ambulatory, with simple setae and stout spines on posteromedial margins (Figs. 9B, C). Pleopod peduncles broader than long, with 3–5 coupling spines and group of proximal plumose setae on medial margins, often with small accessory lobe and simple spine on lateral margins (Figs. 9E–I). Pleopod exopods broader, longer, and with more plumose marginal setae than endopods. Endopod of pleopod 5 naked, proximal medial margin produced, lobelike (Fig. 9I). Appendix masculina rodlike, with simple apex, arising from proximal medial margin of pleopod 2 endopod (Fig. 9F).

## TYPE SPECIES

*Argathona normani* Stebbing, 1905, by monotypy.

## DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

1) *Argathona normani* Stebbing, 1905:17, plate 3A, 1910:100; Richardson, 1910:9; Nierstrasz, 1917:102, 1931:176; Hale, 1925:161; Monod, 1933:180, 1975:1003; Barnard, 1936:156; Bal and Joshi, 1959:565; Pillai, 1967:267; Bruce, 1982a:13.

   **DISTRIBUTION.** Sri Lanka and Bay of Bengal.

2) *Argathona setosa* Richardson, 1910:9, figure 8; Nierstrasz, 1917:102, 1931:175; Hale, 1925: 161; Monod, 1933:182; Bruce, 1982a:23.

   **DISTRIBUTION.** Philippines.

3) *Argathona sulcata* Richardson, 1910:10, figure 9; Nierstrasz, 1917:102, 1931:176; Monod, 1933:181, 1975:1003; Bruce, 1982a:23.

   **DISTRIBUTION.** Philippines.

4) *Argathona macronema* (Bleeker, 1857). For synonymy see Bruce, 1982a:13.

   **DISTRIBUTION.** Throughout the Indo-West Pacific (Bruce, 1982a), including the Red Sea, Gulf of Aqaba, Gulf of Suez, Java, Celebes, Australia, New Guinea, Madagascar, Gilbert Islands, Fiji Islands, and Kenya.

5) *Argathona rhinoceros* (Bleeker, 1857). For synonymy see Bruce, 1982a:14.

   **DISTRIBUTION.** Throughout the Indo-West Pacific, including Aldabra Island, Persian Gulf,

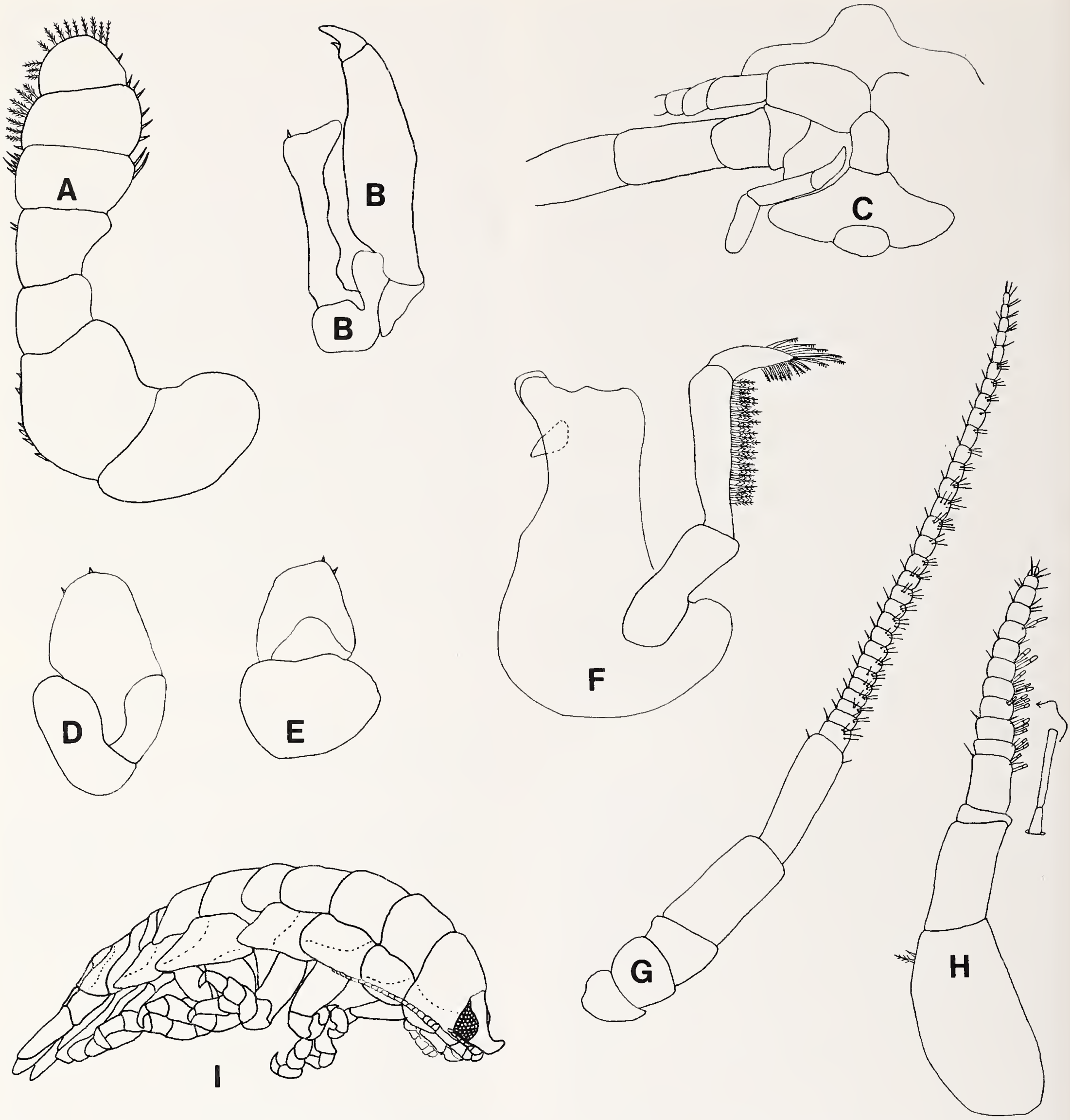


**Figure 7.** *Argathona rhinoceros*, USNM Acc. No. 27085: **A**, maxilliped; **B**, maxillule; **C**, frontal lamina, clypeus, and labrum; **D**, maxilla, dorsal view; **E**, maxilla, ventral view; **F**, mandible; **G**, antenna; **H**, antennule; and **I**, lateral view.

Zanzibar, Sri Lanka, India, Java, Thailand, Australia, Palau Islands, and Eniwetok Atoll.

6) *Argathona confine* Hale, 1925:164, figure 17. *Argathona confinis* Nierstrasz, 1931:176; Monod, 1933:179, 1975:1003; Bruce, 1982a:23 (*lapsus calami*).

**DISTRIBUTION.** Australia.

7) *Argathona parca* Hale, 1940:293, figures 3a–i; Bruce, 1982a:23.

**DISTRIBUTION.** Australia.

8) *Argathona stebbingi* Nierstrasz, 1931:171, figures 58–68; Monod, 1933:182, 1975:1003; Bruce, 1982a:23 (*genus inquirenda*).

**DISTRIBUTION.** Indonesia.

9) *Argathona muraeneae* Bal and Joshi, 1959:563, plate I, figures 1–10; Bruce, 1982a:23 (*genus inquirenda*).

**DISTRIBUTION.** Bombay.

10) *Argathona japonica* Shiino, 1961:93, figures 1, 2; Bruce, 1982a:23.

**DISTRIBUTION.** Japan.

11) *Argathona rostrata* Bruce, 1982a:16, figures 2–4.

**DISTRIBUTION.** Australia.

12) *Argathona crenulata* Bruce, 1982a:20, figures 5, 6.

**DISTRIBUTION.** Australia.

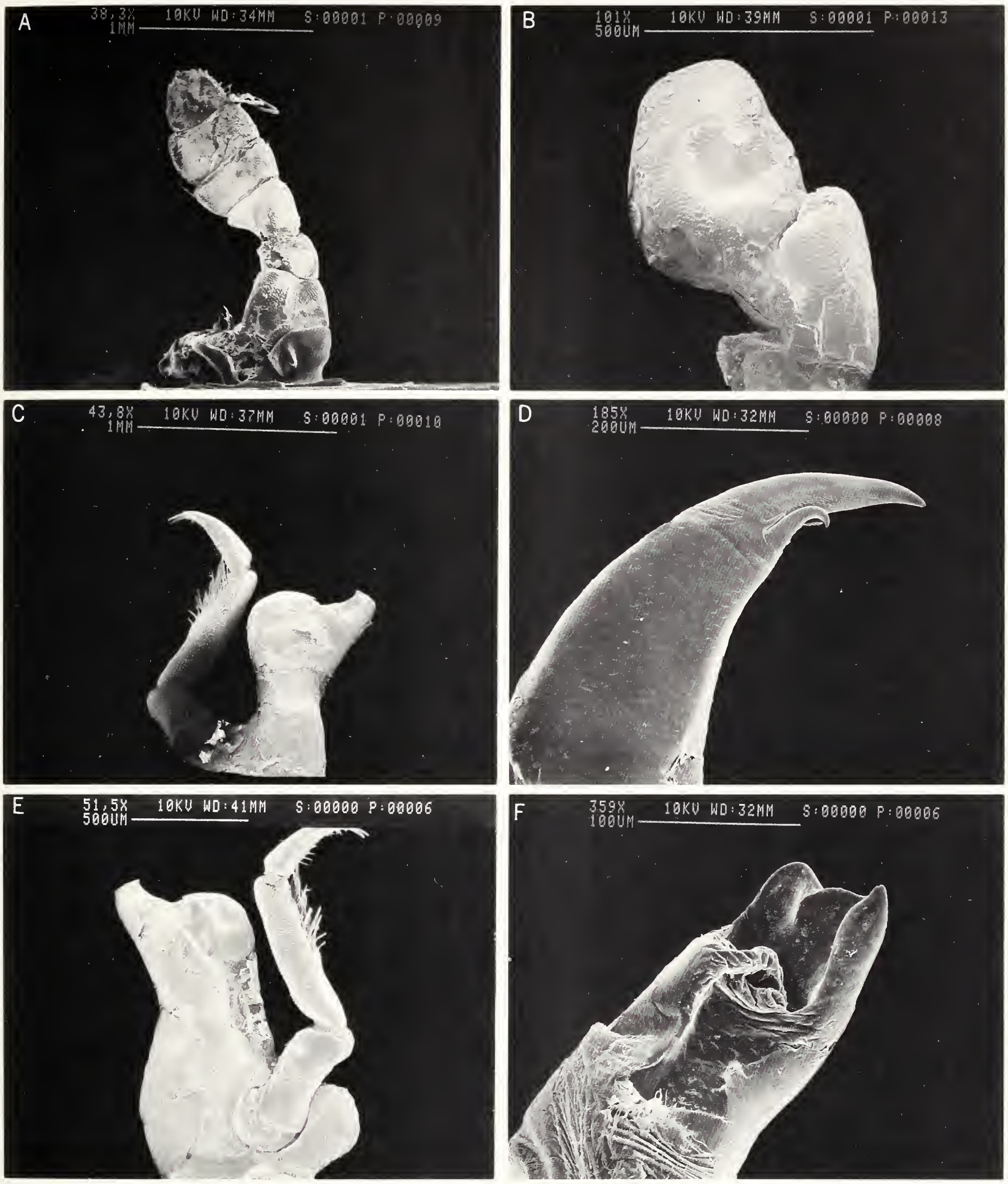

A
38,3X 10KV WD:34MM S:00001 P:00009
1MM
B
101X 10KV WD:39MM S:00001 P:00013
500UM
C
43,8X 10KV WD:37MM S:00001 P:00010
1MM
D
185X 10KV WD:32MM S:00000 P:00008
200UM
E
51,5X 10KV WD:41MM S:00000 P:00006
500UM
F
359X 10KV WD:32MM S:00000 P:00006
100UM

**Figure 8.** Scanning electron micrographs of *Argathona rhinoceros:* **A,** maxilliped; **B,** maxilla; **C,** dorsal view of mandible; **D,** apex of maxillule; **E,** ventral view of mandible; and **F,** apex of mandible.

## REMARKS

The genus *Argathona* was erected by Stebbing (1905) for his new species *A. normani* and was placed in his new family Argathonidae. Hale (1925), Monod (1926, 1976), Barnard (1936), Bal and Joshi (1959), Shiino (1961), Bruce et al. (1982), and Delaney and Brusca (1985) placed *Argathona* in the family Corallanidae. Two species of *Arganotha* (*A. macronema* and *A. rhinoceros*) have been placed, at various times, in 8 different genera (*Aega, Alcirona, Brotherus, Corallana, Cymothoa, Gurida, Livoneca,* and *Orcilana*). In 1911 Stebbing synonymized the genus *Brotherus* with *Argathona.* Monod (1933) synonymized *Orcilana* and *Gurida* with *Argathona.* The most comprehensive treatments of the genus have been those of Monod (1933, 1975) and Bruce (1982a).

The number of accessory spines at the base of the large apical spine on the maxillule varies among different species of *Argathona.* In *A. macronema, A. normani, A. rhinoceros,* and *A. stebbingi* there is usually 1 accessory spine; 2 such spines occur in *A. setosa,* 3 in *A. confine* and *A. sulcata,* and 4 in *A. japonica.*

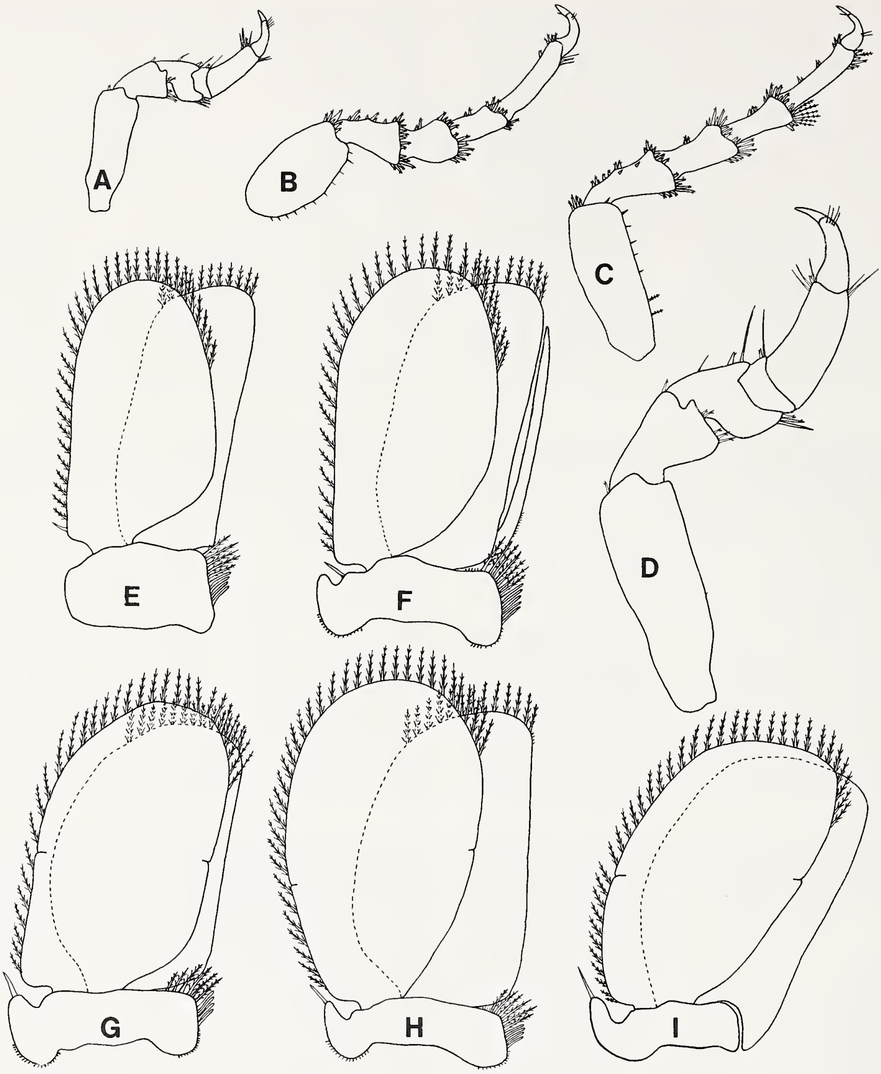


**Figure 9.** *Argathona confine,* USNM 102147: **A,** pereopod I; **B,** pereopod IV; **C,** pereopod VII; **D,** pereopod I, enlarged; **E,** pleopod 1; **F,** pleopod 2; **G,** pleopod 3; **H,** pleopod 4; and **I,** pleopod 5.

The number of maxilliped palp articles in *Argathona* species varies from 4 to 5, usually by complete or partial fusion of articles 2 and 3. In *A. macronema* articles 2 and 3 may be distinct (Monod, 1975:fig. 10) or partly fused (Hale, 1925:fig. 16g). In *A. parca* Hale (1940:fig. 3g), *A. rostrata* Bruce (1982a:figs. 2j, 4g), and *A. crenulata* Bruce (1982a:fig. 5l) the palp is distinctly 4-articulate, with no partial suture evident between articles 2 and 3. Loss or fusion of maxilliped palp articles in *Argathona* has also been reported by Stebbing (1905, 1911), Monod (1933), Barnard (1936), and Pillai (1967). Loss or fusion of maxilliped palp articles also occurs in the corallanid genus *Tachaea* Schioedte and Meinert, 1879, in which fusion of articles is known to differ between the right and left maxillipeds in the same specimen (Tattersall, 1921). Loss and/or fusion of maxilliped palp articles commonly occurs in many other families of isopods.

Two *Argathona* species, *A. stebbingi* Nierstrasz, 1931, and *A. muraeneae* Bal and Joshi, 1959, have been noted above as *genus inquirenda.* As noted by Bruce (1982a), both of these species may belong in *Alcirona,* as they are figured with pereopods, maxillules, and mandibles typical of *Alcirona.* The serrate processes on the dactyli of the anterior pereopods in *A. stebbingi* and *A. muraeneae* are unknown in other *Argathona* species but are figured for *Lanocira zeylanica* (in Monod, 1933:184). That feature and the two large falcate apical spines on the maxillule are features typical of many *Alcirona* species.

Weak sexual variation is evident in the dorsal ornamentation of some *Argathona* species. Females have less-developed rostral processes and ce-

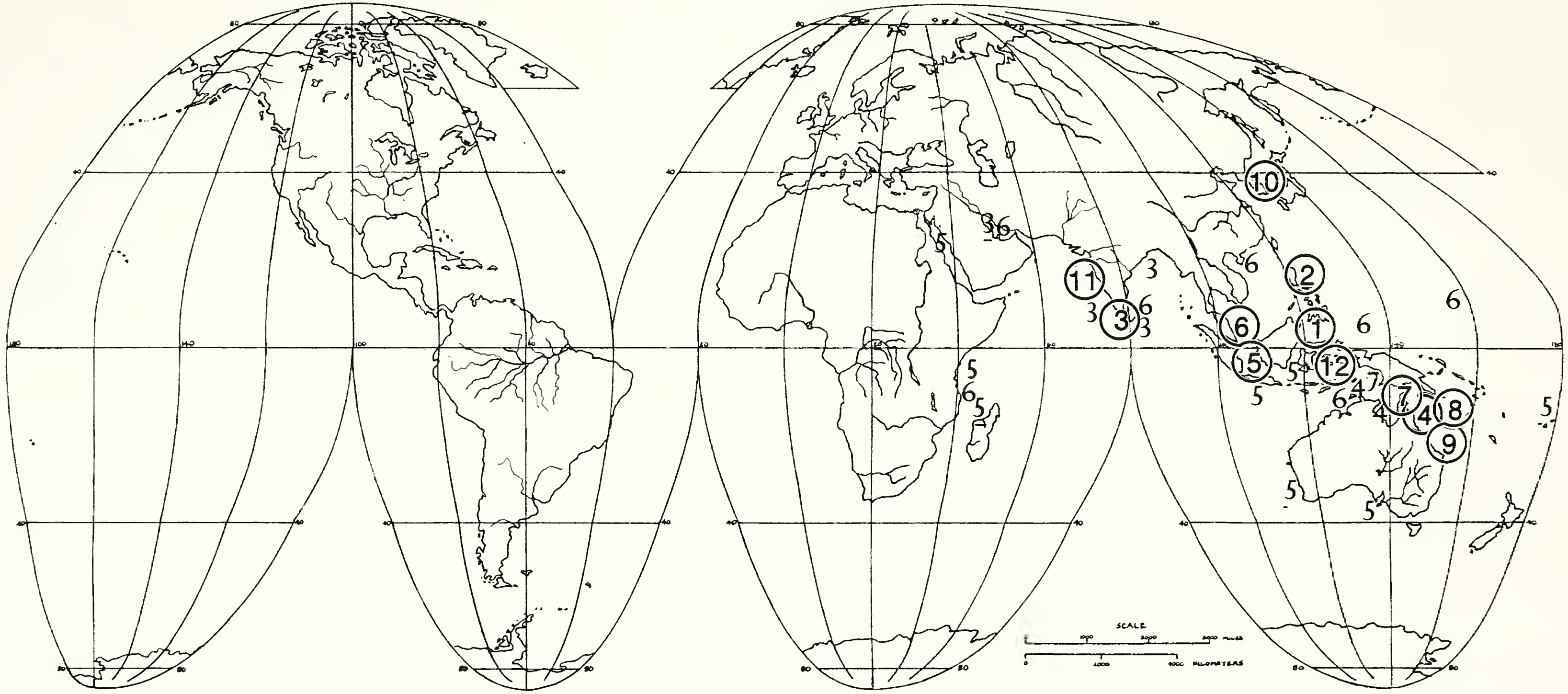


Figure 10. Distribution of *Argathona* species; type localities are circled. Species numbers are: **1,** *A. setosa;* **2,** *A. sulcata;* **3,** *A. normani;* **4,** *A. confine;* **5,** *A. macronema;* **6,** *A. rhinoceros;* **7,** *A. rostrata;* **8,** *A. crenulata;* **9,** *A. parca;* **10,** *A. japonica;* **11,** *A. muraeneae;* and **12,** *A. stebbingi.*

phalic horns in *A. rostrata* and *A. rhinoceros,* respectively. The crenulation of the posterior margins of pereonal and pleonal segments in *A. crenulata* is somewhat less developed in females (Bruce, 1982a). Because of the sexual variation in dorsal ornamentation of some *Argathona* species noted above, females should be identified with care.

Bruce (1982a) notes that adult *A. rostrata* lack a molar process although it is present in juveniles.

### BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The 12 species of *Argathona* are found in tropical/subtropical marine habitats throughout the Indo-West Pacific (Fig. 10) at depths ranging from 8 to 267 m. Five species have been collected as "temporary parasites" of fish: *A. macronema* (from *Epinephelus tauvina, Diagramma cinerascens, Pseudolabras* sp., *Trachichtodes affinis, Cromileptes altivelis, Lutjanus argentimaculata, Plectropoma leopardus,* and *Plectropoma maculatum*); *A. rhinoceros* (from *Tetrodon leopardus, Epinephelus chlorostigma, Epinephelus malabaricus, Epinephelus taurina, Variola louti,* and *Plectropoma leopardus*); *A. parca* (from "eye of Queensland Grouper"); *A. muraeneae* (from *Muraena tessellata*); and *A. confine* (from "blue-spotted lagoon ray"). *Argathona macronema* has been reported from the eye of the sea turtle *Chelonia mydas* (by Monod, 1975). *Argathona macronema, A. setosa, A. rostrata,* and *A. crenulata* have been collected from among coral reef rock and from coral rubble and sand. *Argathona parca* and *A. rostrata* have been reported from sponges, and *A. confine* from *Comatula* sp.

## Genus *Corallana* Dana, 1853

*Corallana* Dana, 1853:773; Milne-Edwards, 1840: 237; Heller, 1868:143; Schioedte and Meinert, 1879:286; Miers, 1881:78; Hansen, 1890:379; Stebbing, 1893:315, 1904a:13, 1904b:699; Richardson, 1900b:157; Moore, 1902:169; Barnard, 1914:358; Nierstrasz, 1917:101, 1930:1, 1931:163; Monod, 1934:1; Barnard, 1955:59; Pillai, 1954:6, 1961:49, 1967:272; Roman, 1970:167; Kensley, 1978:75; Bruce, 1982b:241; Bruce et al., 1982: 464; Jones et al., 1983:837; Delaney and Brusca, 1985:728.

Non *Corallana:* Miers, 1881:78; Hansen, 1890:280; Richardson, 1900b:157; Moore, 1902:169 (= *Excorallana* Stebbing, 1904a).

### MATERIAL EXAMINED

*Corallana hirsuta:* 1) Laccadive Islands, Minikoi, BMNH 1928.12.: 1542–1551, 18 fe. and 14 ma. *Corallana africana:* 1) South Africa, Port Elizabeth, Zwartkops River, BMNH 1927.5.31: 71–75 (part) (syntypes), 4 ma., 4.4, 4.6, 5.2, and 5.2 mm. *Corallana nodosa:* 1) Sri Lanka, Lake Negombo, BMNH 1928.12.1: 1598–1600, 1 spec. (heavily dissected), 8.8 mm; 2) Siam, Koh Kut, USNM Acc. No. 107725, "from jar H.M. Smith, Siam," 7 fe. and 3 ma.; 3) Siam, Koh Kut, USNM Acc. No. 107725, "from prawn," 1 fe. *Corallana furcilla:* 1) Siam, Koh Kut, USNM Acc. No. 107725, "from jar H.M. Smith, Siam," 11 fe; 2) Philippine Islands, Aklan, New Washington, Tambuntingi Fishpond, USNM Acc. No. 271086, "isopods parasitic on *Chanos chanos,*" 5 fe. *Corallana tridentata:* 1) Papua New Guinea, Port Moresby, BMNH 1982: 219:3 (part) (paratypes), 1 fe., 7.2 mm, and 1 ma., 7.2 mm. *Corallana bidentata:* 1) Papua New Guinea, Port Moresby, BMNH 1982: 221:3 (part) (paratypes), 1 fe., 12.4 mm, and 1 ma., 14 mm; 2) Australia, Queensland, Brisbane River, Kangaroo Point, AM No. P10691, "from submerged timber," 1981, 3 fe., 7.2, 8.2, 8.8, and 1 ma., 7.6 mm. *Corallana estuaria:* 1) Australia, Brisbane, BMNH 1921.3.23: 80–82, 2 fe., 8.0 and 12.0 mm, and 1 ma., 10.0 mm; 2) Papua New Guinea, Port Moresby, USNM Acc. No. 320977, "from wood," 1 fe. and 1 ma. *Corallana* spp.: 1) Siam, Bangkok, USNM Acc. No. 142233, "isopods parasitic on skin of *Puntius javanicus,*" 2 fe., 3 ma., and 1 manca; 2) Eniwetok, Parry Island, USNM Acc. No. 197874, coll. H.S. Ladd, No. 1539, "from rounded block," 3 fe. and 2 ma.; 3) West Pacific, Japtan Island, USNM Acc. No. 197874, coll. H.S. Ladd, No. 1523, "seaward," 1 fe.; 4) Singapore, St. John's Island, CAS No. 025344, "bottom: rocks and mud," 3 fe., 7.6 (gravid), 8.0, and 12.0 mm; 5) Australia, Hinchabrook Island, Nina Bay, "from rotting log in brackish creek," 2 fe. and 1 juvenile; 6) Australia, Queensland, Torres Strait, Prince of Wales Island, Off Bampfield Head, AM No. P28783, coll. CSIRO Coast Prawn Fisheries Project, "beam trawl over seagrass beds, time 1250 hrs.," 2 fe., 5.9 and 6.2 mm; 7) Australia, Queensland, near Lizard Island, 1 mile SW of Eagle Island, AM No. P28790, LI-61, depth 4–91 m, "sponge sample with some algae and coral rubble," 1 manca, 3.5 mm.

### DIAGNOSIS

Antennule peduncle 2- or 3-articulate; basal article of peduncle enlarged. Frontal lamina shape various, ovoid, triangular, pentagonal, or quadrangular, but not elongate; reduced or absent in some species. Clypeus short, small, not encompassing small labrum, or crescent-shaped and partly encompassing small labrum. Mandible with short incisor (long in *Corallana kulai* and C. sp. Bruce, 1982b); incisor bi- or tricuspid; molar process small, lacinia mobilis small or absent. Maxillule lateral lobe apex with 1 large falcate spine; medial lobe simple, blunt. Maxilla 2-articulate, rounded lobe. Maxilliped very narrow, without endite; basis very elongate, length 2.0–4.0 times width; palp always 5-articulate, middle palp article not elongate (except in C. sp. Bruce, 1982b). Anterior pereopods without serrate dactyli and propodi; carpi not produced on posteromedial margins ("inner angles") as in *Tachaea.*

### ADDITIONAL DESCRIPTION

Corallanidae with eyes well developed, at lateral margins of cephalon. Dorsum often with tubercles and setae (Fig. 1C). Antennule peduncle basal article enlarged (Fig. 11F). Clypeus varies from short and small to inverted V- or semilunar shape, may or may not encompass small labrum (Figs. 12D, F). Mandible palp inserted near base, 3-articulate; middle article longest, all articles with comblike cuticular structures, middle and distal articles with ctenate marginal setae (Figs. 11A, 12E, G, H, 13B–F). Maxillule lateral (outer) lobe slender, tapering to form single, large falcate spine (Figs. 11C, 13A, 14E, F); some specimens of *Corallana* sp. (USNM 142233) have 1 minute, straight spine at base of large spine. Maxilla apex with 0–1 simple seta, occasionally with comblike cuticular structures (Figs. 11B, 14D). Maxilliped palp apical article and medial margins of other articles with short simple setae (Figs. 11D, E, 14A–C). Pereopods I–III subprehensile, with simple setae and robust spines on posteromedial margins (Fig. 12A). Pereopods IV–VII longer, ambulatory, with stout spines and setae on posteromedial margins (Figs. 12B, C). Pleopod peduncles broader than long, with 3–4 coupling spines and group of proximal setae on medial margins, and with simple spine on lateral margins (Figs. 15A–E). Exopods of pleopods broader, longer, with more plumose marginal setae than endopods. Endopods of pleopods 3–4 naked or with reduced setation in some species (Figs. 15C, D). Endopod of pleopod 5 naked, proximal medial margin produced, lobelike (Fig. 15E). Male pleopod 2 with rodlike appendix masculina, with simple apex, arising from proximal medial margin of endopod (Fig. 15B). Pleotelson lateral margins often bisinuate, apex bluntly rounded or truncate. Uropodal exopods often elongate, narrow, with longitudinal keel (Fig. 1C).

## TYPE SPECIES

*Corallana hirticauda* Dana, 1853:774, plate 51, figures 8a–c, by monotypy. Bruce (1982b:241, citing T.E. Bowman, personal communication) states that type specimens of the type-species have not been located and were probably lost when the sloop 'Peacock' sank off the mouth of the Columbia River in 1841.

## DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

1) *Corallana hirticauda* Dana, 1853:774, plate 51, figures 8a–c; Schioedte and Meinert, 1879: 287; Hansen, 1890:388; Stebbing, 1893:315, 1904a:13, 1904b:705; Richardson, 1900b:157; Nierstrasz, 1917:101, 1931:163; Bruce, 1982b: 241; Jones et al., 1983:845.

**DISTRIBUTION.** Tongatabu, Philippines.

2) *Corallana hirsuta* Schioedte and Meinert, 1879: 287, table V, figure 11; Stebbing, 1904a:13, 1904b:704; Nierstrasz, 1931:163; Monod, 1934:1; Barnard, 1955:59; Bruce, 1982b:243; Jones et al., 1983:845.

**DISTRIBUTION.** Philippines, Maldives, and Indochina.

3) *Corallana collaris* Schioedte and Meinert, 1879: 287, table V, figures 1, 2; Nierstrasz, 1931: 165; Bruce, 1982b:248; Jones et al., 1983:845.

**DISTRIBUTION.** Philippines.

4) *Corallana brevipes* Schioedte and Meinert, 1879: 287, table V, figures 3, 4; Nierstrasz, 1931: 165; Bruce, 1982b:248; Jones et al. 1983:845.

**DISTRIBUTION.** Philippines.

5) *Corallana nodosa* Schioedte and Meinert, 1879: 287, table V, figure 7; Stebbing, 1904a:13; Nierstrasz, 1931:165; Barnard, 1955:59; Pillai, 1954:6, 1961:49, 1967:272; Bruce, 1982b:282; Jones et al., 1983:845.

**DISTRIBUTION.** Philippines, Sri Lanka, India, Australia, and Papua New Guinea.

6) *Corallana basalis* (Heller, 1868:143, table XII, figures 14, 14a); Schioedte and Meinert, 1879: 287; Nierstrasz, 1931:165; Bruce, 1982b:248.
*Aega basalis* Heller, 1868.

**DISTRIBUTION.** Nicobar Islands, Indian Ocean.

7) *Corallana sculpta* (Milne-Edwards, 1840:237); Bruce, 1982b:248.
*Cirolana sculpta* Milne-Edwards, 1840.

**DISTRIBUTION.** Malabar, India.

8) *Corallana africana* Barnard, 1914:358, plate XXX, figure D; Nierstrasz, 1931:165; Roman, 1970:167; Kensley, 1978:75; Bruce, 1982b:242; Jones et al., 1983:845.

**DISTRIBUTION.** South Africa and Madagascar.

9) *Corallana leopoldi* (Nierstrasz, 1930:1); Bruce, 1982b:248.
*Tachaea leopoldi* Nierstrasz, 1930:1.

**DISTRIBUTION.** Aroe Islands, Moluccas.

10) *Corallana glabra* Nierstrasz, 1931:163, figures 30–37; Bruce, 1982b:248.

**DISTRIBUTION.** Kei Islands, Arafura Sea.

11) *Corallana furcilla* Barnard, 1955:59, figures 28c–e; Kensley, 1978:75; Bruce, 1982b:248; Jones et al., 1983:845.

**DISTRIBUTION.** Inhambane, Mozambique; Siam; and Philippines.

12) *Corallana kulai* Bruce, 1982b:243, figures 2, 3; Jones et al., 1983:845.

**DISTRIBUTION.** Western Australia.

13) *Corallana* sp. Bruce, 1982b:246, figures 4a–i.

**DISTRIBUTION.** New Guinea.

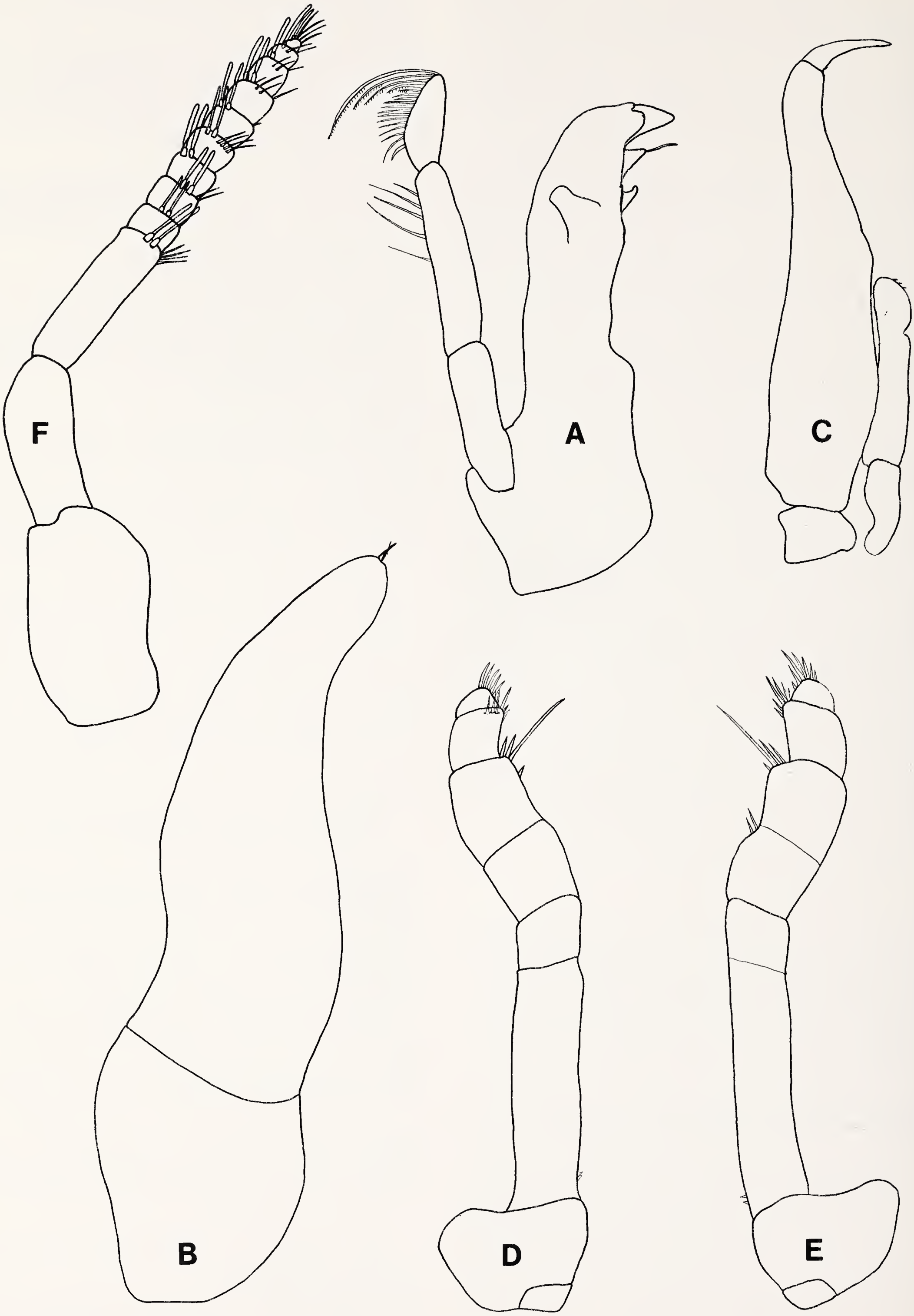


Figure 11. *Corallana* sp., USNM Acc. No. 142233: **A,** mandible; **B,** maxilla; **C,** maxillule; **D,** right maxilliped; **E,** left maxilliped; and **F,** antennule.

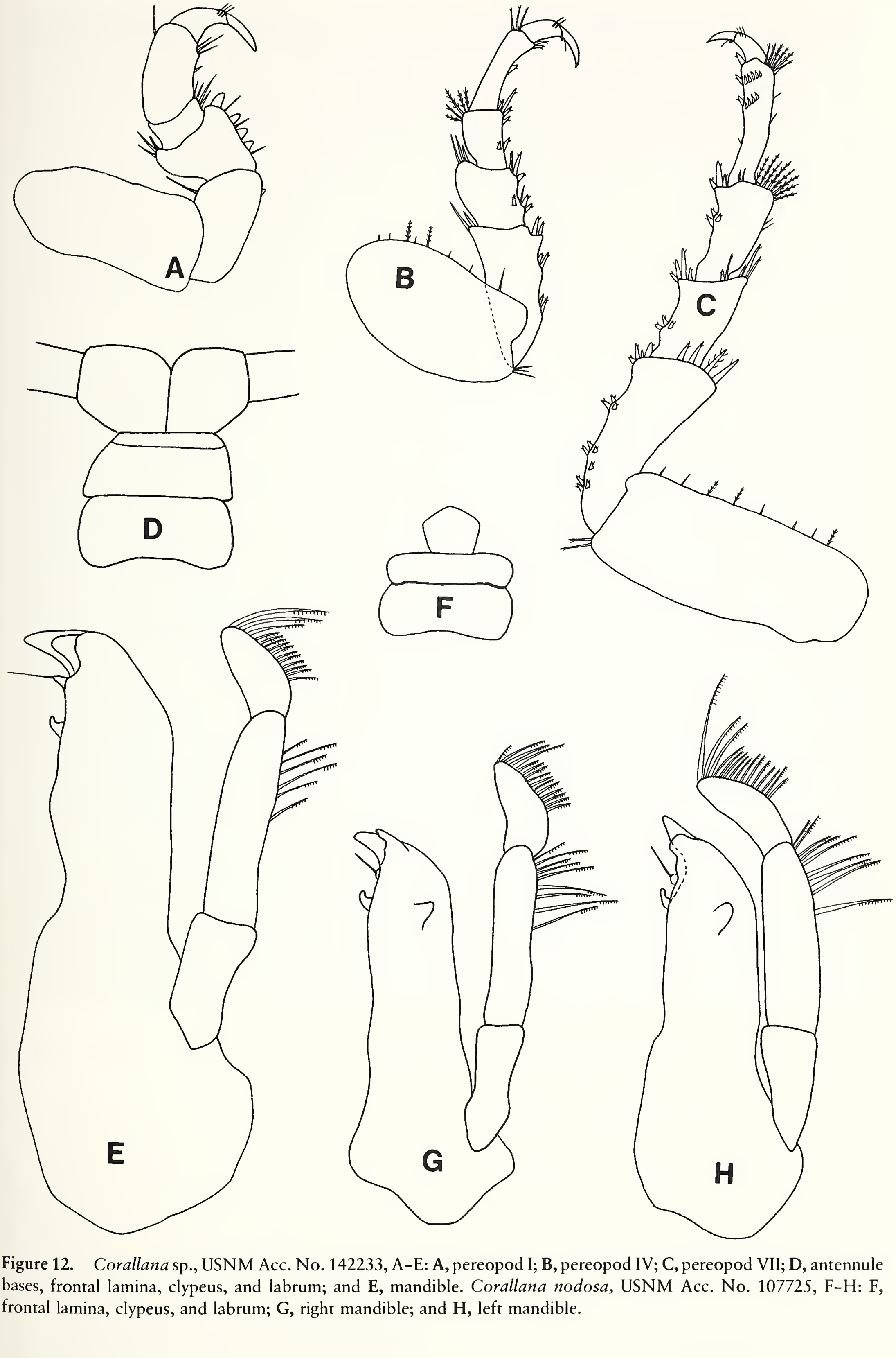


Figure 12. *Corallana* sp., USNM Acc. No. 142233, A–E: **A,** pereopod I; **B,** pereopod IV; **C,** pereopod VII; **D,** antennule bases, frontal lamina, clypeus, and labrum; and **E,** mandible. *Corallana nodosa,* USNM Acc. No. 107725, F–H: **F,** frontal lamina, clypeus, and labrum; **G,** right mandible; and **H,** left mandible.

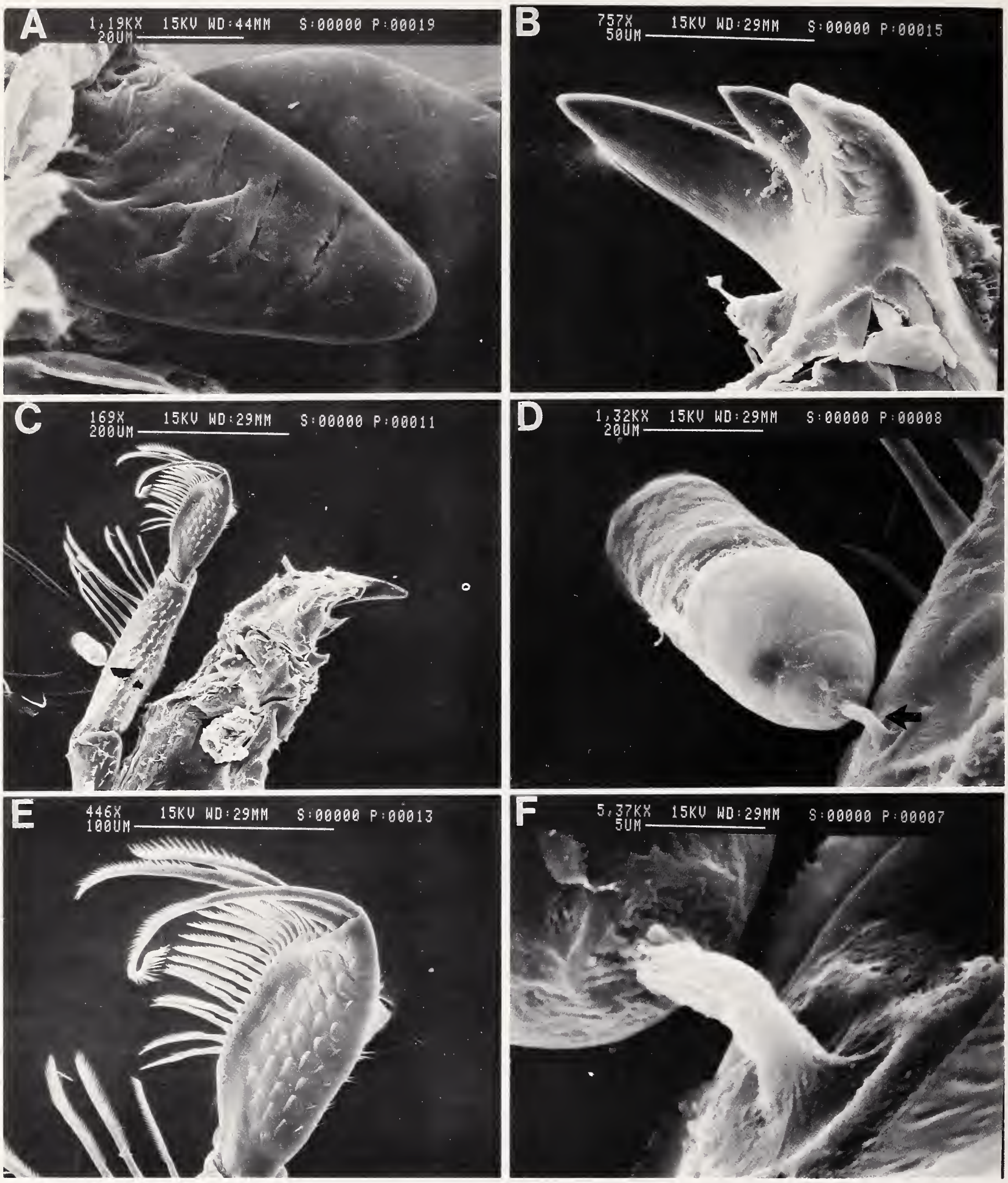

A
1,19KX 15KV WD:44MM S:00000 P:00019
20UM
B
757X 15KV WD:29MM S:00000 P:00015
50UM
C
169X 15KV WD:29MM S:00000 P:00011
200UM
D
1,32KX 15KV WD:29MM S:00000 P:00008
20UM
E
446X 15KV WD:29MM S:00000 P:00013
100UM
F
5,37KX 15KV WD:29MM S:00000 P:00007
5UM

**Figure 13.** Scanning electron micrographs of *Corallana estuaria,* USNM Acc. No. 320977: **A,** apex of medial lobe of maxillule; **B,** mandible apex; **C,** mandible; **D,** parasitic protozoan on mandibular palp (arrow in C); **E,** distal article of mandibular palp; and **F,** detail of protozoan attachment to palp (arrow in D).

14) *Corallana estuaria* Jones et al., 1983:837, figures 1a–n.

**DISTRIBUTION.** Papua New Guinea and Queensland, Australia.

15) *Corallana bidentata* Jones et al., 1983:840, figures 2a–n.

**DISTRIBUTION.** Papua New Guinea.

16) *Corallana tridentata* Jones et al., 1983:842, figures 3a–n.

**DISTRIBUTION.** Papua New Guinea.

## REMARKS

The genus *Corallana* was erected by Dana (1853) to house his new species *Corallana hirticauda.* Bruce (1982b) and Jones et al. (1983) noted the need for a thorough revision of *Corallana.* Both studies noted that a great deal of variation in the morphology of the mouthparts, frontal lamina, and clypeus exists in this genus. Variation is notably evident in the *Corallana* "sp." partly described but not named by Bruce (1982b). Some *Corallana* type material has been lost, and many of the earlier species

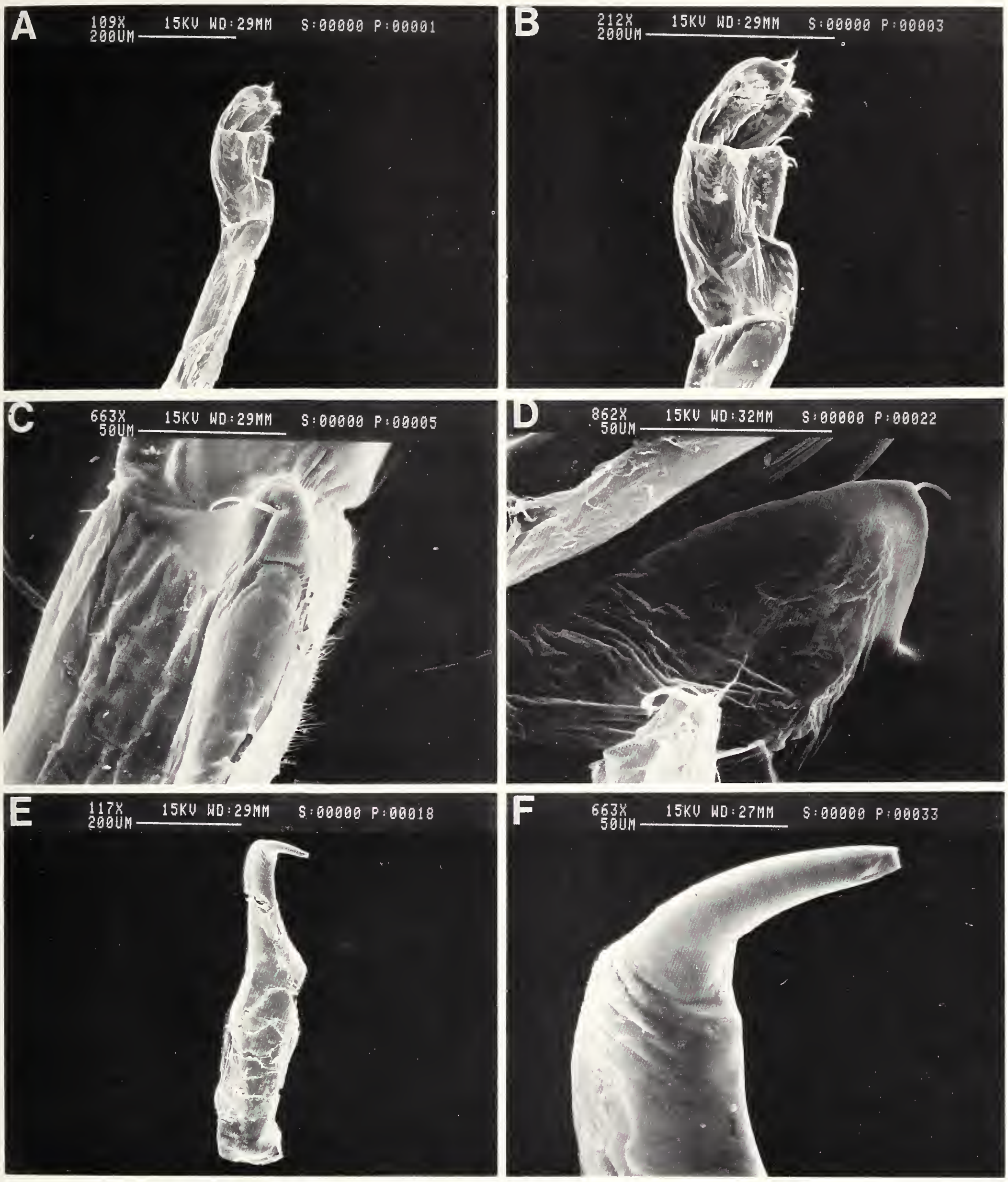

A
109X 15KV WD:29MM S:00000 P:00001
200UM
B
212X 15KV WD:29MM S:00000 P:00003
200UM
C
663X 15KV WD:29MM S:00000 P:00005
50UM
D
862X 15KV WD:32MM S:00000 P:00022
50UM
E
117X 15KV WD:29MM S:00000 P:00018
200UM
F
663X 15KV WD:27MM S:00000 P:00033
50UM

**Figure 14.** Scanning electron micrographs of *Corallana estuaria,* USNM Acc. No. 320977: **A,** maxilliped palp; **B,** detail of distal palp articles; **C,** detail of maxilliped basis; **D,** maxilla apex; **E,** maxillule; and **F,** maxillule apex.

descriptions are poor or incomplete; some lack any figures whatsoever.

In the description of *Corallana bidentata* Jones et al., 1983, the figures of the mandible, maxilliped, frontal lamina, clypeus, and labrum resemble those of *Tachaea.* The holotype was not examined by the present author, however, so this species must remain in *Corallana* for the present.

Sexual dimorphism in dorsal ornamentation exists in some *Corallana* species. As is usually the case in corallanid species, males often possess much more distinct tuberculation and ornamentation than do females, including cephalic, pereonal, and pleonal tuberculation, and an upwardly produced basal article on the antennule peduncle. In some *Corallana* species, however, females are known to possess characters of ornamentation lacking in males. For example, in *C. furcilla* adult females have a pair of distinct apical processes or "prongs" on the pleotelson, which are apparently absent in males.

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The 16 species of *Corallana* are restricted to marine and brackish- (low salinity) water habitats in the

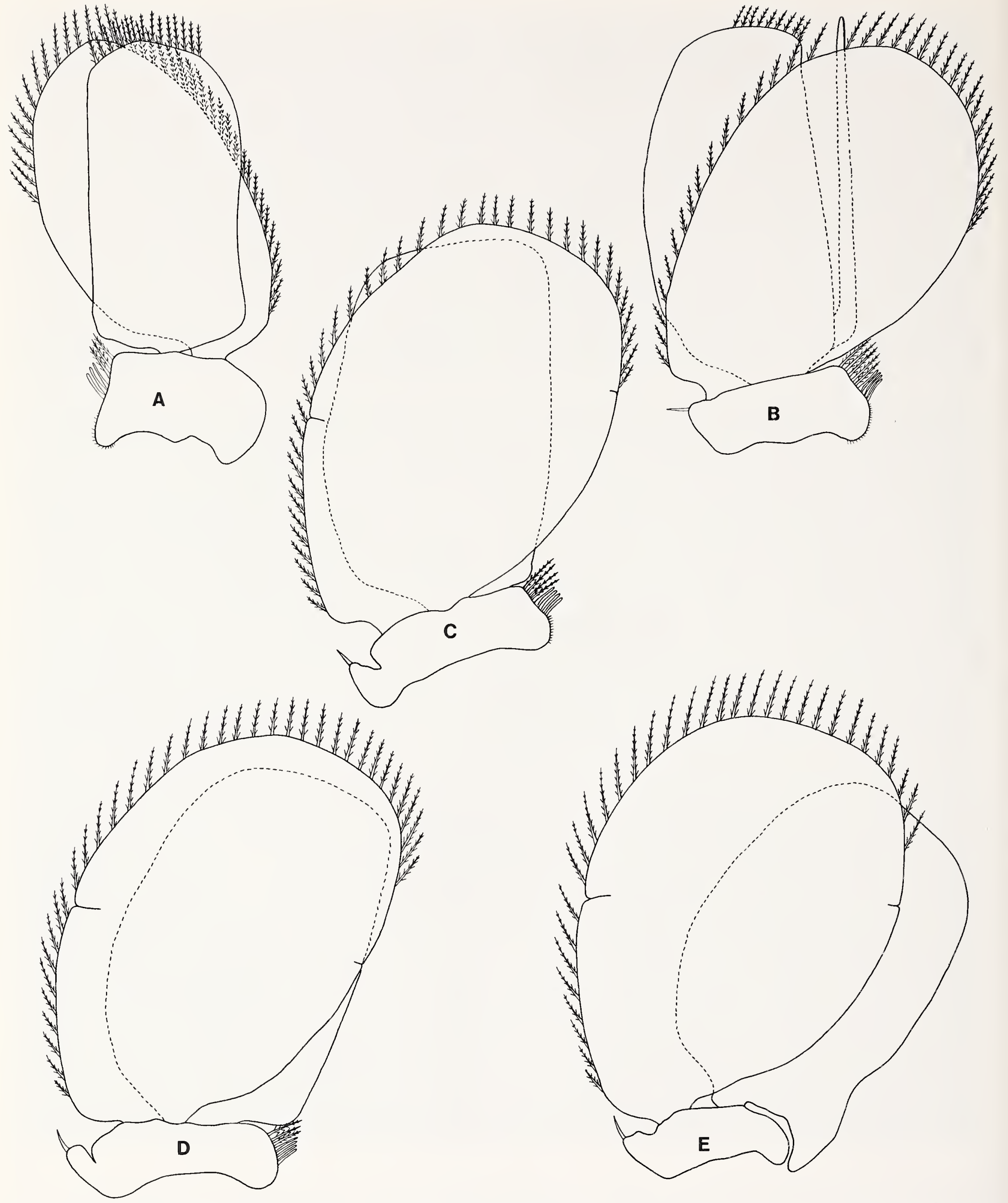


**Figure 15.** *Corallana* sp., USNM Acc. No. 142233: **A,** pleopod 1; **B,** pleopod 2; **C,** pleopod 3; **D,** pleopod 4; and **E,** pleopod 5.

Indo-West Pacific (Fig. 16) at depths ranging from the intertidal zone to 150 m. Six species are described as being "from wood" in estuarine or brackish-water habitats—either from rotting logs, mangrove prop roots, pier pilings, or treated wood test panels, in their own burrows or in those of other wood borers such as *Limnoria* sp., *Sphaeroma terebrans,* and *S. triste.* Wood used for burrowing by *Corallana* species includes *Avicennia eucalyptifolia, Rhizophora stylosa* (prop roots), and *Alstonia scholaris* (treated test panels) (see Jones et al., 1983).

Jones et al. (1983) discussed the wood-boring species of *Corallana* and noted that some of these *Corallana* species occurred in small colonies of about 20 individuals each in man-made wood structures and in larger colonies in mangrove stumps (*C. nodosa*), although *C. bidentata* occurred only singly or in pairs.

*Corallana* species have been reported from a variety of other hosts and substrates. *Corallana hirticauda* was found on dead coral (Dana, 1853); *C. bidentata* in the pneumatophores of *Sonneratia*

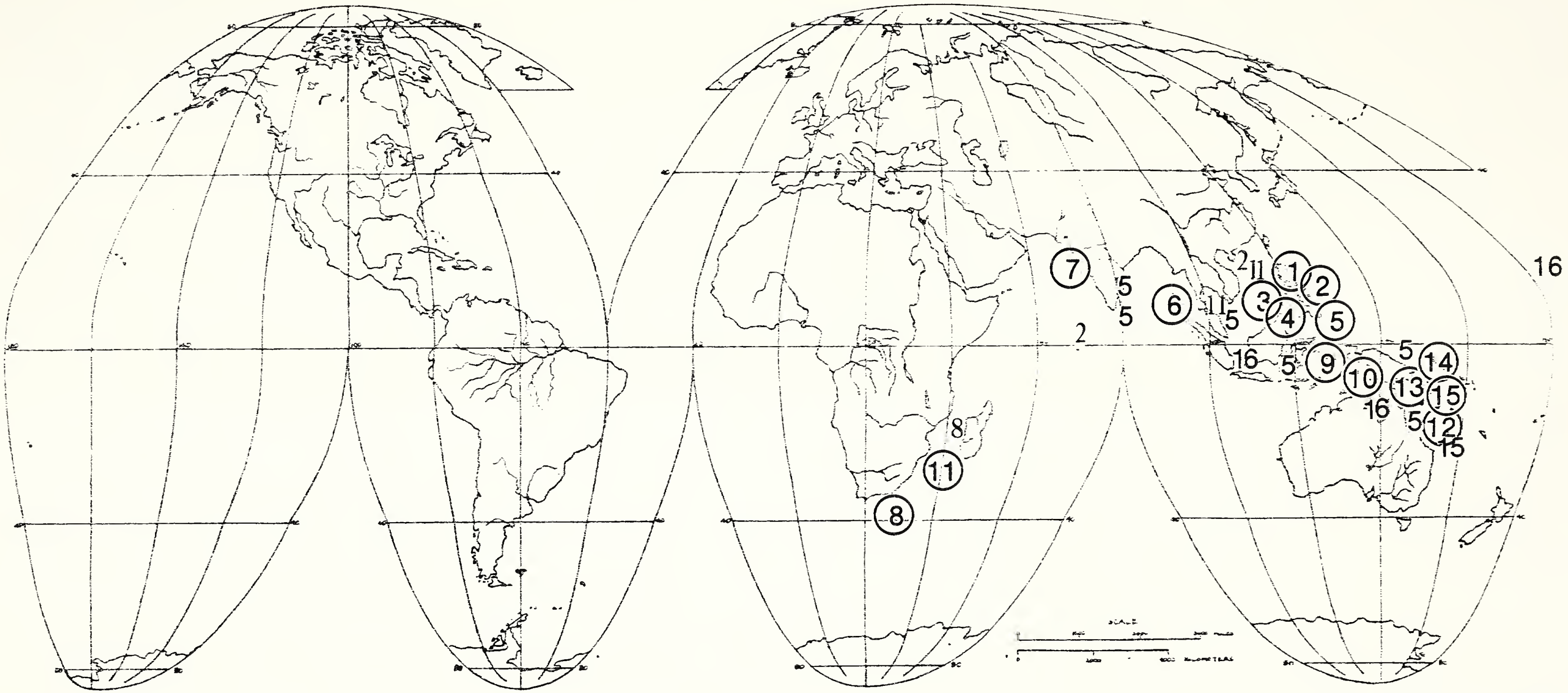


Figure 16. Distribution of *Corallana* species; type localities are circled. Species numbers are: **1,** C. *hirticauda;* **2,** C. *hirsuta;* **3,** C. *collaris;* **4,** C. *brevipes;* **5,** C. *nodosa;* **6,** C. *basalis;* **7,** C. *sculpta;* **8,** C. *africana;* **9,** C. *leopoldi;* **10,** C. *glabra;* **11,** C. *furcilla;* **12,** C. *kulai;* **13,** C. *tridentata;* **14,** C. *estuaria;* **15,** C. *bidentata;* and **16,** C. sp.

*alba* (Jones et al., 1983); and other *Corallana* species on rocks/mud, with sponge, algae, and coral, and in beam trawls over seagrass beds. *Corallana furcilla* has been collected as a "parasite" from *Chanos chanos* in a fishpond in the Philippines, *Corallana* sp. as a "parasite" from the fish *Puntius javanicus* in Siam, and *C. nodosa* "from prawn" at Lake Negombo, Sri Lanka.

## Genus *Excorallana* Stebbing, 1904a

*Excorallana* Stebbing, 1904a:13, 1904b:703; Lemos de Castro, 1960:64, 1964:3; Menzies and Glynn, 1968:42; Monod, 1969:48; Carvacho and Yanez, 1971:129; Delaney, 1982:273; Bruce et al., 1982:464; Delaney, 1984:1; Delaney and Brusca, 1985:728.

*Exocorallana* Richardson, 1905:138 (*lapsus calami*).

### MATERIAL EXAMINED

*Excorallana acuticauda:* 1) South Atlantic Ocean, Hotspur Bank, BMNH 1880:30, holotype, H.M.S. *Alert,* depth 63 m, 17°32′S, 35°45′W, Leg. Lords of the Admiralty, 1 fe.; 2) Brazil, Alagoas, Maceio, USNM 25821, Branner-Agassiz Expedition, "from coral reef," 1 ma. and 1 fe.; 3) Florida, Loggerhead Key, N.W. of lighthouse, USNM (no Acc. No.), 4 Aug 1924, coll. W.L. Schmitt, depth 3–5 m, 1 ma.; 4) Florida, Loggerhead Key, USNM Acc. No. 68708, 1 ma.; 5) Florida, USNM Acc. No. 15488, Manter #778, from *Prianthus crentatus,* "dynamite," 1 fe. (gravid); 6) Brazil, Pernambuco, USNM 43676, 1 spec.; 7) Florida, Loggerhead Key, N.W. of lighthouse, USNM (no Acc. No.), 4 Aug. 1924, coll. W.L. Schmitt, depth 3–9 m, 1 ma.; 8) Florida, Tortugas, White Shoals, USNM Acc. No. 84129, Sta. 18, 1 fe.; 9) Florida, Tortugas, White Shoals, USNM Acc. No. 84129, col. W.L. Schmitt, Sta. 22, 1 fe.; 10) (as *Excorallana antillensis*), West Indies, St. Thomas, ZMUC syntype, 1 ma.; 11) (as *E. antillensis*), West Indies, ZMUC syntype, 1 fe.; 12) (as *E. antillensis*), West Indies, ZMUC syntype, 1 ma.; 13) West Indies, U.S. Virgin Islands, St. Croix, N.E. coast, 23 March 1982, KK-1982, coll. K. Kleeman, "taken at 10 m on forereef in empty bivalve burrows with other *Excorallana* species and unidentified cirolanids," 1 ma. and 1 fe.; 14) West Indies, U.S. Virgin Islands, St. Croix, 7 June 1983, ACM-1983, coll. A.C. Miller, "off rocks at 16 m depth," 1 ma.; 15) Florida, Biscayne Key, USNM 45956, 2 fe.; 16) West Indies, St. Thomas, USNM 87072, *Albatross,* Sta. 7667, 1 fe.; 17) Puerto Rico, Luis Pena Channel, USNM 406, coll. Johnson-Smithsonian Deep-Sea Expedition, "with 8′ net and cargo light over ship's side," 3 fe.; 18) West Indies, Virgin Islands, St. Thomas, USNM 111384, 1 spec.; 19) Puerto Rico, Crashboat Basin, USNM 119486, "from stomach of *Odontoscion denter,* depth 3–4 m," 1 spec. *Excorallana tricornis tricornis:* 1) Florida, Tortugas, USNM 68375, "from red grouper *Epinephelus,*" 6 ma. and 23 fe.; 2) West Indies U.S. Virgin Islands, St. Croix, N.E. coast, KK-1982, 23 March 1982, "taken at 10 m on forereef from empty bivalve burrows with other *Excorallana* spp. and cirolanids," coll. K. Kleeman, 8 ma. and 15 fe.; 3) West Indies, ZMUC syntypes, 305 spec.; 4) Central America, "Reialeio," ZMUC, 1 fe.; 5) West Indies U.S. Virgin Islands, St. Croix, ZMUC syntype, coll. Orsted, 1 fe.; 6) West Indies, ZMUC syntypes, 3 ma. and 2 fe.; 7) West Indies, St. Thomas, ZMUC syntypes, 2 fe.; 8) Florida, USNM Acc. No. 93400, Sta. 6, 1 ma. and 1 fe.; 9) Florida, USNM Acc. No. 93400, "living in tubular bryozoan from piles at Fort," 1 ma. and 1 fe.; 10) Florida, Tortugas, USNM Acc. No. 115488, "Night—found on table where Hartman was cutting up fish taken from trap on west side Loggerhead Key," 1 ma.; 11) Florida, Tortugas, Loggerhead Key, USNM (no Acc. No.), 1 ma., 1 fe., and 1 juvenile; 12) Florida, Tortugas, USNM (no Acc. No.), June 1925, "with polychaetes," coll. Dexter, 1 ma.; 13) Florida, Tortugas, Loggerhead Key, USNM (no. Acc. No.), 21 July 1924, "from rocks west of Lighthouse," coll. W.L. Schmitt, 1 fe.; 14) Florida, Tortugas, USNM Acc. No. 115488, "from outside head region and within buccal cavity of Nassau Grouper, taken in trap," 4 ma. and 10 fe.; 15) Florida, W. side of Bush Key Reef, near Long Key, USNM Acc. No. 84129, "from holes in rocks, 1 m depth," 1 ma.; 16) Florida, Tortugas, Loggerhead Key, off northern end, USNM Acc. No. 84129, 1 ma. and 1 fe.; 17) West Indies, USNM Acc. No. 208263, Sta. 106-56, 1 ma.; 18) Caribbean Sea, Saba Bank, USNM Acc. No. 208263, Sta. 106-56, "from princess rockfish *Mycteroperca bowersi* at 12.5 m depth," 12 spec.; 19) Puerto Rico, off Puntilla Point, USNM Acc. No. 142536, Sta. 19, depth 6–7 m, 5 spec.; 20) Puerto Rico, San Juan, USNM Acc. No. 142536, Sta. 21, "mangrove swamp," coll. Smithsonian-Hartford Expedition, 2 spec.; 21) Caribbean Sea, Isla Roatan, S.W. corner of island, RCB-1978, "living in yellow sponge, taken via SCUBA coll. on reef," coll. R.C. Brusca, 1 ma. *Excorallana tricornis occidentalis:* 1) Mexico, Gulf of California, Baja California Sur, Isla San Francisco, AHF 518-36, "with 3 *Excorallana houstoni,*" coll. R/V *Velero III,* 1 ma.; 2) Mexico, Gulf of California, Baja California Norte, San Felipe, USNM Acc. No. 150937, 3 June 1934, "from holes in red beach sponges," 15 spec.; 3) Gulf of California, Baja California Norte, San Felipe, USNM Acc. No. 144660, "on gorgonians," 1 spec.; 4) Gulf of California, Baja California, Isla Tiburon, Bahia Red Bluff, USNM Acc. No. 150937, 75+ spec.; 5) Gulf of California, Baja California Sur, Isla Espiritu Santo, San Lorenzo Channel, USNM Acc. No. 139772, #60736, "corallines," depth 43 m, 1 ma.; 6) Gulf of California, Baja California Sur, Cabo San Lucas, USNM 86383, 19 July 1938, "from external and nostril of Gulf grouper, fish #1," 2 ma. and 19 fe.; 7) Gulf of California, Bahia Concepcion, USNM 86381, 1 fe.; 8) Ecuador, La Libertad, USNM 68438, Sta. 10-33, 1 fe. (cephalon damaged); 9) Mexico, Jalisco, Bahia Coastocomate, 60 km N.N.W. of Manzanillo, Colima, USNM Acc. No. 28194, RAD-68-I, "inside empty *Gastrochaena* valves," depth 3–20 m, 20 spec.; 10) Mexico, Jalisco, Bahia Espiritu Santo, Playa Paraiso, USNM Acc. No. 281954, RAD-68-II, depth 5–10 m, 1 ma. and 3 fe.; 11) Mexico, Sonora, Puerto Penasco, AHF 1010-01, 2 fe.; 12) Costa Rica, Isla Cano, HG-1984, "with 280 micron dip net at 23:54 hours," coll. H. Guzman, Universidad de Costa Rica, 3 ma., 4 fe., and 2 mancas; 13) Costa Rica, Isla Cano, HG-1984, "with 280 micron dip net at 23:45 hours," coll. H. Guzman, Universidad de Costa Rica, 2 ma., 4 fe., and 5 mancas. *Excorallana houstoni:* 1) Galapagos Islands, Isla Santa Cruz, Academy Bay, Nelson's Landing, CAS 02544, "taken intertidally," 1 ma.; 2) Galapagos Islands, Isthmo Perry, Elizabeth Bay, Penguin Rocks, LACM (no Acc. No.), 23 May 1970, "intertidal rocks," coll. L.T. and V. Williams, 1 fe.; 3) Mexico, Gulf of California, Baja California Sur, Cabo San Lucas, Cabeza Ballena, AHF (no Acc. No.), 9 Nov 1946, Dawson Sta. 53, "at 7 a.m., water temp. 26.6°C," coll. E.Y. Dawson, 1 ma. and 1 fe.; 4) Mexico, Gulf of California, Baja California Sur, Isla San Francisco, AHF 518-36, "littoral—with 1 ma. *E. tricornis occidentalis*," coll. R/V *Velero III*, 1 ma. and 2 fe.; 5) Galapagos Islands, Nameless Island, WDH-330765, Sta. 26A, 22 Feb 1978, "intertidal, with 25+ *Dynamenella* sp.," coll. W.D. Hope, 1 fe. *Excorallana bruscai:* 1) Mexico, Gulf of California, Baja California Sur, Isla Espiritu Santo, Bahia San Gabriel, USNM 144492, #634-37, "shore," 1 ma. and 3 fe. (2 gravid); 2) Mexico, Gulf of California, Sonora, Puerto Penasco, AHF 1006-01, "rocky intertidal," 1 ma.; 3) Mexico, Sonora, Puerto Penasco, AHF 1004-01, holotype 6611, "from sand beach in evening, using seine," 1 ma.; 4) Mexico, Sonora, Puerto Penasco, PMD-1981, 19 April 1981, "found inside white sponge *Leucetta losangelensis* with *Paracerceis sculpta,* in low intertidal," coll. P.M. Delaney, 1 ma.; 5) Mexico, Gulf of California, Baja California Sur, Bahia Concepcion, EWI-1980, "from subtidal coralline algae," coll. E.W. Iverson, 1 ma.; 6) Mexico, Sonora, Puerto Penasco, Cholla Bay, UA68-139, 1 ma.; 7) Mexico, Sonora, Puerto Penasco, Cholla Bay, AHF 1007-01, "on mud of low intertidal," 1 ma.; 8) Mexico, Sonora, Puerto Penasco, Station Beach, PP-ZI-129-21, 23 April 1979, "infauna of coquina reef," coll. P. Pepe, 4 ma. and 3 fe.; 9) Mexico, Sonora, Puerto Penasco, Station Beach, PP-ZII-51-83, "inside *Serpulorbis margaritaceous* tubes," coll. P. Pepe, 4 ma. and 1 fe. *Excorallana subtilis:* 1) West Indies, St. Thomas, ZMUC holotype, 1 juvenile; 2) Florida, Key West Harbor, USNM 13581, #614, 2 ma. *Excorallana truncata:* 1) Mexico, Baja California, Kellett Channel, S. of Cedros Island, LACM 71-159, "depth 36 m, pebbles and shale," R/V *Searcher,* 1 fe. (gravid); 2) Mexico, Gulf of California, Sonora, Puerto Penasco, PP-ZI-129-49, 26 Jan 1979, "cryptofauna of coquina reef," coll. P. Pepe, 1 ma. and 1 fe.; 3) California, Santa Monica Bay, AHF 1636-1, Sta. 13, #1, "depth 64–66 m, coarse sand," 1 fe.; 4) Mexico, Baja California, Thurloe Head, USNM Acc. No. 128938, #283-34, "depth 14–18 m, dredging off Thurloe Pt.," 1 ma.; 5) California, Point Fermin, USNM Acc. No. 112912, #168, 1 ma.; 6) Mexico, Gulf of California, USNM (no Acc. No.), 25 March 1889, Sta. 3024, "depth 20 m," coll. R/V *Albatross,* 2 spec.; 7) Mexico, Baja California, Bahia San Quintin, USNM Acc. No. 139772, #488, "sand and seaweed," 1 ma.; 8) Mexico, Baja California, Isla Cerros, S. Bay, USNM Acc. No. 128938, "dredging at depth 18–26 m," 1 fe. *Excorallana berbicensis:* 1) Surinam (Dutch Guiana), Clevia Estate, USNM 60286, "from Clevia waterside," 1 ma. and 2 fe.; 2) British Guiana, Rio Berbice, USNM 50402 (types), Feb 1913, 2 spec. *Excorallana mexicana:* 1) Florida, Hillsborough Co., 104 km W. of Egmont Key, USNM 170833, Hourglass Cruises, Sta. 66-443, depth 55 m, coll. R/V *Hernan Cortez,* 1 ma.; 2) Florida, Hillsborough Co., 104 km W. of Egmont Key, USNM 330682, depth 55 m, coll. Hourglass Cruises, 1 fe.; 3) Florida, Hillsborough Co., 104 km W. of Egmont Key, Hourglass Cruises, Sta. 66-109, depth 55 m, 1 fe.; 4) Gulf of Mexico, USNM 9601, Sta. 2369-2374, depth 45–49 m, coll. U.S. Fish Commission Steamer *Albatross,* 3 ma.; 5) Gulf of Mexico, USNM 9601, Sta. 2406, coll. R/V *Albatross,* 1 ma.; 6) Gulf of Mexico, USNM 20479, Sta. 2405, coll. R/V *Albatross,* 2 spec.; 7) Gulf of Mexico, USNM 20478, Sta. 2369-74, R/V *Albatross,* 11 spec.; 8) Gulf of Mexico, USNM 9814, Sta. 2407, R/V *Albatross,* 2 ma.; 9) Dutch West Indies, Orangested, USNM Acc. No. 142536, Sta. 46, 1 ma.; 10) Northwest Atlantic Ocean, off Florida, USNM 211835, "by trawl at depth 53.7 m," 1 ma.; 11) Florida, between delta of Mississippi River and Cedar Keys, USNM 39420, Sta. 2369-74, depth 45–49 m, 11 ma. and 8 fe.; 12) Florida, between delta of Mississippi River and Cedar Keys, USNM 32074 (holotype), Sta. 2406, depth 47 m, coll. R/V *Albatross,* 1 ma. *Excorallana oculata:* 1) West Indies, ZMUC syntypes, 1 ma. and 1 fe.; 2) Brazil, off Cape St. Roque, USNM 43648, Sta. 2578, depth 36 m, coll. R/V *Albatross,* 1 ma.; 3) Brazil, off Cape St. Roque, USNM 32246, Sta. 2758, depth 36 m, coll. R/V *Albatross,* 1 ma. and 1 fe.; 4) West Indies, U.S. Virgin Islands, St. Croix, N.E. coast, KK-1982, 23 March 1982, "taken at 10 m depth on forereef in empty bivalve burrows with other *Excorallana* spp. and cirolanids," coll. K. Kleeman, 2 ma. and 1 fe. (gravid); 5) West Africa, Cameroon, S.W. of Annobon, near Fernando Poo Island, USNM 119468, Sta. 282, depth 18–38 m, coll. Pillsbury, 7 spec.; 6) West Indies, Barbados, English Harbor, USNM 53886, "taken using electric light," 1 ma.; 7) West Indies, Barbados, English Harbor, USNM 86377, #25289, "collected with electric light," 2 ma.; 8) Caribbean Sea, Puerto Rico, off Playa de Fajardo, USNM 90436, Sta. 358/67, "captured with circular net and electric cargo light at anchorage," coll. Johnson-Smithsonian Deep-Sea Expedition, 1 fe.; 9) West Africa, Congo, Ile. Annobon, ZMHUB, OM 29, "taken at 50–60 m with trawl or dredge," coll. A. Crosnier, 40+ spec. *Excorallana quadricornis:* 1) West Indies, St. Thomas, ZMUC syntypes, 1 ma. and 1 fe.; 2) West Indies, ZMUC syntype, 1 fe.; 3) Brazil, USNM 91435, #1.316, "Isopods from Museo Paulista, Brazil," 5 ma. and 10 fe.; 4) Puerto Rico, San Juan, USNM Acc. No. 142536, Sta. 21, "mangrove swamp," coll. Smithsonian-Hartford Expedition, 1 ma.; 5) West Indies, U.S. Virgin Islands, St. Croix, Mangrove Island, USNM Acc. No. 142536, Sta. 37, coll. Smithsonian-Hartford Expedition, 1 ma. and 2 fe.; 6) Jamaica, Montego Bay, Bogue Islands, USNM 52163, "from red sponge on mangrove roots," 3 ma.; 7) Jamaica, Montego Bay, Bogue Islands, USNM 41806, "from red sponge on mangrove roots," 33 spec.; 8) Venezuela, Isla Aves, USNM 154534, "isopods from fish or on copulatory scars of sea turtle *Chelonia mydas,*" 1 ma. and 1 fe.; 9) No locality, USNM Acc. No. 283626, RAD-68-I, coll. G.E. Radwin, 1 ma. and 12 fe.; 10) West Indies, Martinique, St. Luce, USNM Acc. No. 277606, "parasites from *Harpe rata,*" 1 ma., 2 fe., and 1 juvenile; 11) Jamaica, Montego Bay, Bogue Islands, USNM 41808, "orig. No. 26," "commensal on black ascidian on mangrove roots," 1 ma. and 1 fe. (gravid). *Excorallana sexticornis:* 1) Puerto Rico, Caballo Blanco Reef, USNM 44243, coll. steamer *Fish Hawk,* 1 ma.; 2) Florida, Key West, USNM 13540 (types), 1 ma. and 8 fe. *Excorallana warmingii:* 1) Cuba, off southern coast, USNM Acc. No. 198858, #786, "dip net under night light," coll. R/V *Oregon,* 1 ma.; 2) Puerto Rico, Luis Pena Channel, USNM 90439, Sta. 79, #406, "taken with 8′ net and cargo light over ship's side," coll. Johnson-Smithsonian Deep-Sea Expedition, 6 fe.; 3) Caribbean Sea, USNM 9590, Sta. 2365, coll. R/V *Albatross,* 1 fe. (most of pleon and pleotelson missing); 4) Atlantic Ocean, ZMUC holotype, 17°47′N, 35°16′W, 1 ma.; 5) Atlantic Ocean, ZMUC, 17°43′N, 64°56′W, "sta. 1281 X, 50 M.W., 11:30 p.m.," 1 ma.; 6) Florida, Loggerhead Key, USNM Acc. No. 68708, "off wharf," 1 fe.; 7) Florida, Tortugas, S. of Loggerhead Key, USNM Acc. No. 68708, "surface tow, 7 min. S. of wreck to wreck, 5 a.m.," 1 fe.; 8) Florida, Tortugas, Loggerhead Key, USNM Acc. No. 68708, "plankton, 5 a.m.," 1 fe. *Excorallana fissicauda:* 1) West Indies, ZMUC holotype, 1866, 1 fe.

## DIAGNOSIS

Antennule peduncle 2- or 3-articulate; basal article of peduncle expanded. Frontal lamina narrow, shape various; clypeus and labrum very broad and short. Mandible with elongate, falcate incisor; molar process and lacinia mobilis small or absent. Maxillule lateral lobe forming single large recurved spine; medial lobe simple, with bluntly rounded apex. Maxilla forming simple lobe with bi- or trifid apex. Maxilliped palp always 5-articulate, middle article elongate (length = 2× width); maxilliped basis not elongate. Anterior pereopods without serrate dactyli or propodi; carpi not produced.

## ADDITIONAL DESCRIPTION

Corallanidae with eyes well developed, often contiguous at midline of cephalon, or nearly so. Body often with dorsal setae, spines, tubercles, or carinae; dorsum often with setae in pits and globate sockets (Figs. 1D, 17, 18A–D). Ventral and medial surfaces of antennules, antennae, frontal lamina, clypeus, labrum, and mouthparts often with many comb- and scalelike cuticular structures of 5–10 micrometer dimensions (Figs. 17, 20–23). Antennule peduncle basal article enlarged (Figs. 17C, 19D, 20A, C). Antenna peduncle articles 4 and 5 elongate (Figs. 19E, 20A). Frontal lamina, clypeus, and labrum (Figs. 20A–D, 21G) visible anterior to mandibles, but may be partly obscured by same. Mandible palp 3-articulate, middle and distal articles with plumose marginal setae; left and right mandibles interdigitate (Figs. 20A, 21A, B, 22A–C). Maxillule lateral lobe forming single large recurved spine; medial lobe simple (Figs. 21C, 22A, C, 23A). Maxilla apex bi- or trilobed (Figs. 21E, 23A–D). Maxilliped palp middle article elongate (length = 2× width) (Figs. 21D, 22A, D–F). Pereopods I–III subprehensile, with short blunt spines on posterior medial margins of meri and ischia (Figs. 18E, F, 19A). Pereopods IV–VII longer, ambulatory, with spines and setae; propodi not dilated as in *Tachaea* (Figs. 19B, C). Peduncles of pleopods 1–4 with 4–6 coupling spines on medial margin and group of plumose setae ventral to spines, lateral margins with simple spine (Figs. 24A–E). Peduncles of pleopods 2–5 often with small lobe on lateral margins. All rami of all pleopods setigerous. Male pleopod 2 with rodlike appendix masculina arising from proximal medial margin of endopod (Fig. 24B). Pleotelson with lateral incisions in many species (Fig. 1D).

## TYPE SPECIES

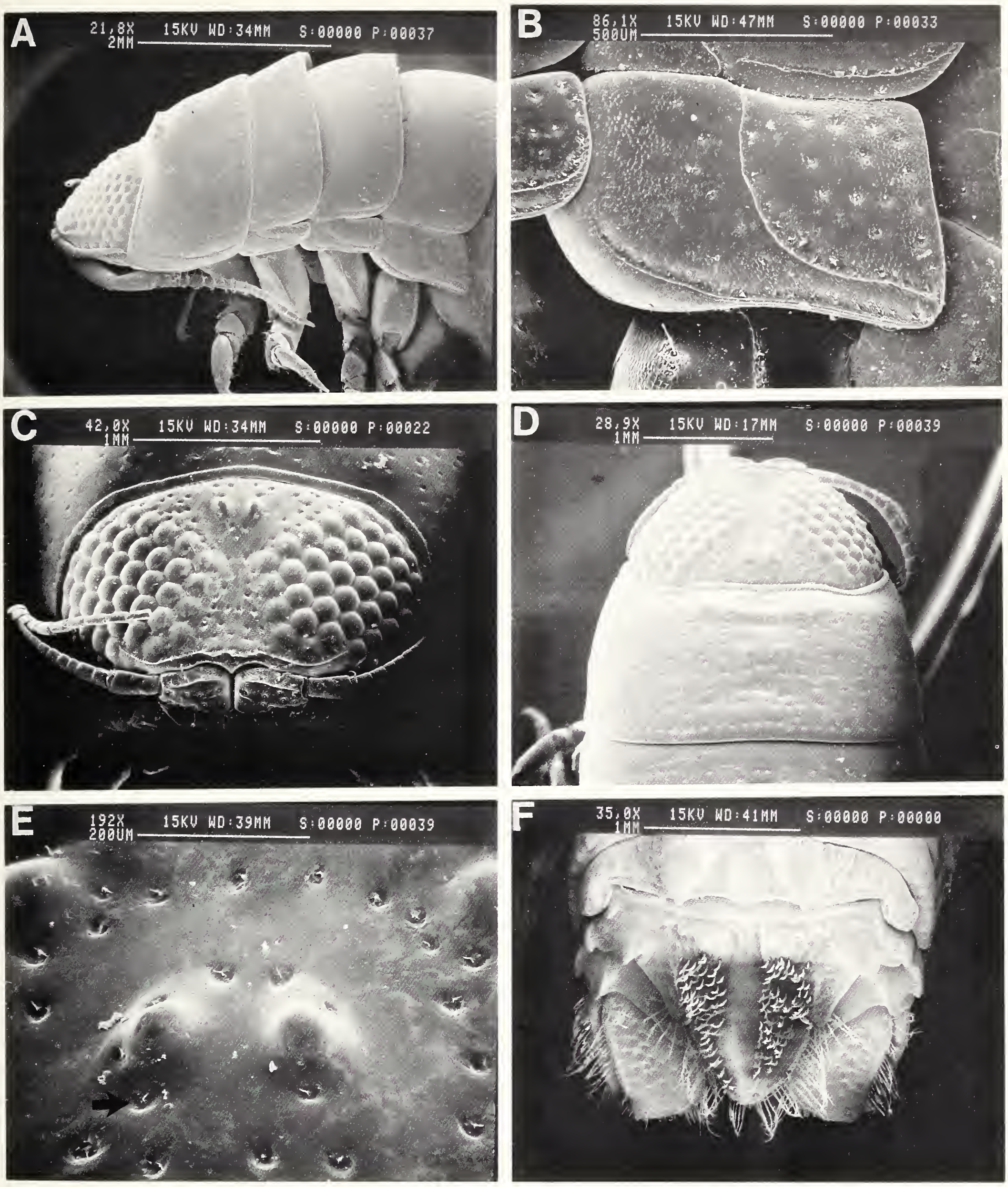
*Excorallana tricornis tricornis* (Hansen, 1890), originally described as *Corallana tricornis,* by designation (Delaney, 1984:2).

## DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

1) *Excorallana tricornis tricornis* (Hansen, 1890): 379, table VI, figures 4a–p, table VII, figures 1a–d; Lemos de Castro, 1960:61, 1964:4; Hutton, 1964:447; Menzies and Glynn, 1968: 11; Monod, 1969:50; Carvacho and Yanez, 1971:130; Moreira and Sadowsky, 1978:107; Menzies and Kruczynski, 1983:70; Kensley, 1984:33; Delaney, 1984:3.

   *Exocorallana tricornis tricornis* Richardson, 1905:139, 1912:188; Rouse, 1969:133 (*lapsus calami*).

   *Corallana tricornis* Hansen, 1890:379; Stebbing, 1893:315; Richardson, 1901:517; Moore, 1902:169; Nierstrasz, 1917:101.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B
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C
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1MM
D
28,9X 15KV WD:17MM S:00000 P:00039
1MM
E
192X 15KV WD:39MM S:00000 P:00039
200UM
F
35,0X 15KV WD:41MM S:00000 P:00000
1MM

**Figure 17.** Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: **A,** anterolateral view; **B,** coxa IV; **C,** anterior view of cephalon; **D,** dorsal view of cephalon and pereonite I (arrow points to tubercle pair); **E,** tubercle pair (from D) surrounded by cuticular sensillae in "pits"; and **F,** dorsal setae and lateral incisions on pleotelson.

DISTRIBUTION. Gulf of Mexico and Caribbean.

2) *Excorallana houstoni* Delaney, 1984:11, figures 5–7, 20, 21.

DISTRIBUTION. Central Gulf of California, western Mexico, and Galapagos Islands.

3) *Excorallana bruscai* Delaney, 1984:5, figures 1–4, 14–17, 22.

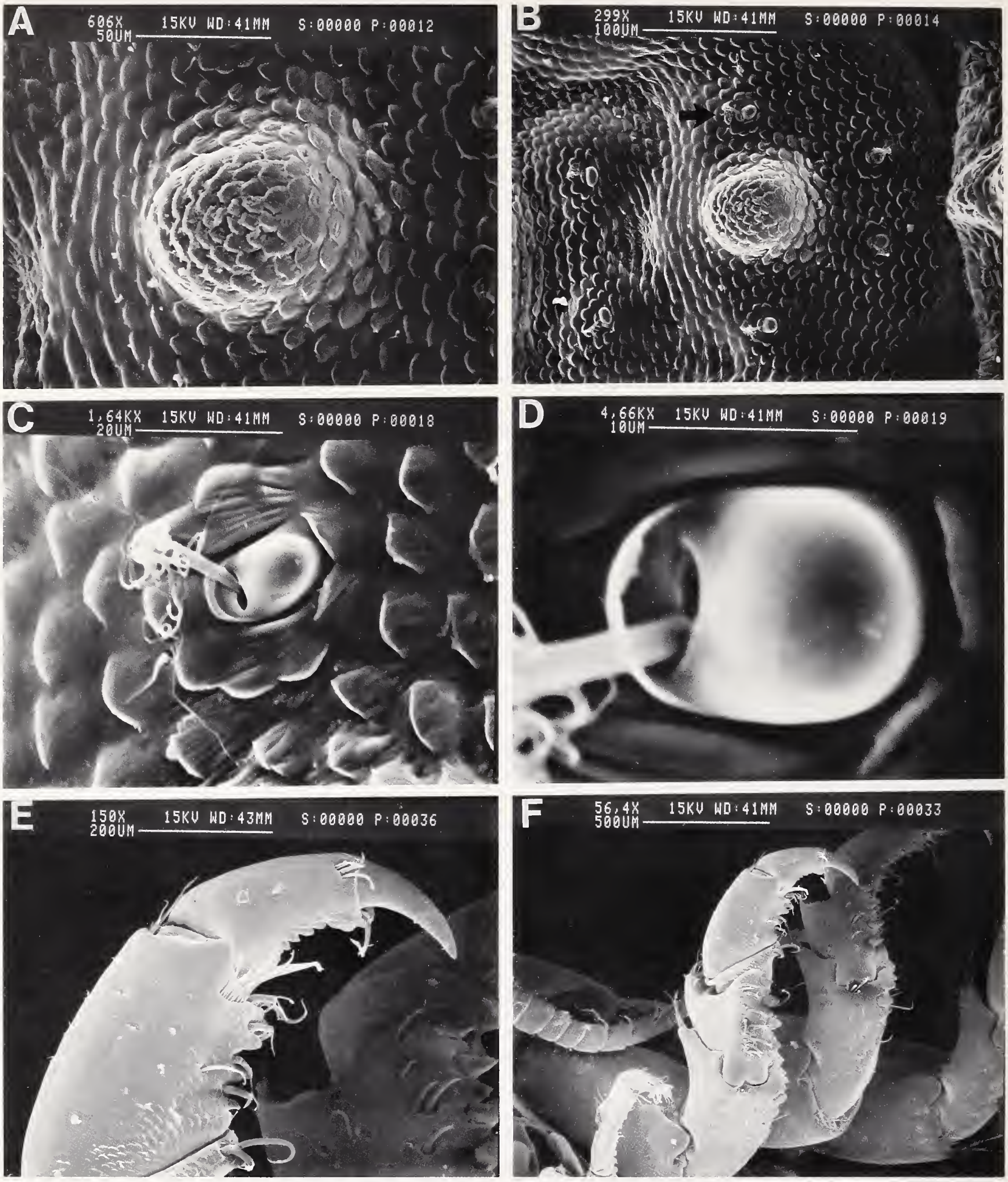
DISTRIBUTION. Gulf of California.

4) *Excorallana acuticauda* (Miers, 1881):78, plate VII, figure 13; Lemos de Castro, 1960:61, 1964: 3; Monod, 1969:48; Carvacho and Yanez, 1971:129; Delaney, 1984:3.

*Corallana acuticauda* Miers, 1881:78; Hansen, 1890:388; Nierstrasz, 1917:101.

*Excorallana antillensis* (Hansen, 1890):383; Lemos de Castro, 1960:61, 1964:4; Monod, 1969: 48; Carvacho and Yanez, 1971:129; Menzies and Kruczynski, 1983:75; Delaney, 1984:3.

*Exocorallana antillensis* Richardson, 1905:148 (*lapsus calami*).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20UM
D
4,66KX 15KV WD:41MM S:00000 P:00019
10UM
E
150X 15KV WD:43MM S:00000 P:00036
200UM
F
56,4X 15KV WD:41MM S:00000 P:00033
500UM

**Figure 18.** Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: **A,** median tubercle on pleonite 5; **B,** six cuticular structures around tubercle; **C,** one pleonal cuticular structure; **D,** detail of cuticular structure; **E,** pereopod I, propodus, and dactyl; and **F,** pereopod I.

*Corallana antillensis* Hansen, 1890:383; Richardson, 1901:517; Nierstrasz, 1917:101.

**DISTRIBUTION.** Caribbean and Brazil.

5) *Excorallana subtilis* (Hansen, 1890):382, table VII, figures 3a–e; Boone, 1921:93; Lemos de Castro, 1960:61, 1964:4; Miller, 1968:17; Monod, 1969:49; Carvacho and Yanez, 1971: 130; Delaney, 1984:3.
*Exocorallana subtilis* Richardson, 1905:146 (*lapsus calami*).
*Corallana subtilis* Hansen, 1890:382; Richardson, 1901:517; Nierstrasz, 1917:101.

**DISTRIBUTION.** Caribbean.

6) *Excorallana tricornis occidentalis* Richardson, 1905:141, no figures; Monod, 1969:50; Bowman, 1977:657; Delaney, 1984:13.

**DISTRIBUTION.** Southwestern Baja California, Gulf of California, and western Mexico south to Panama.

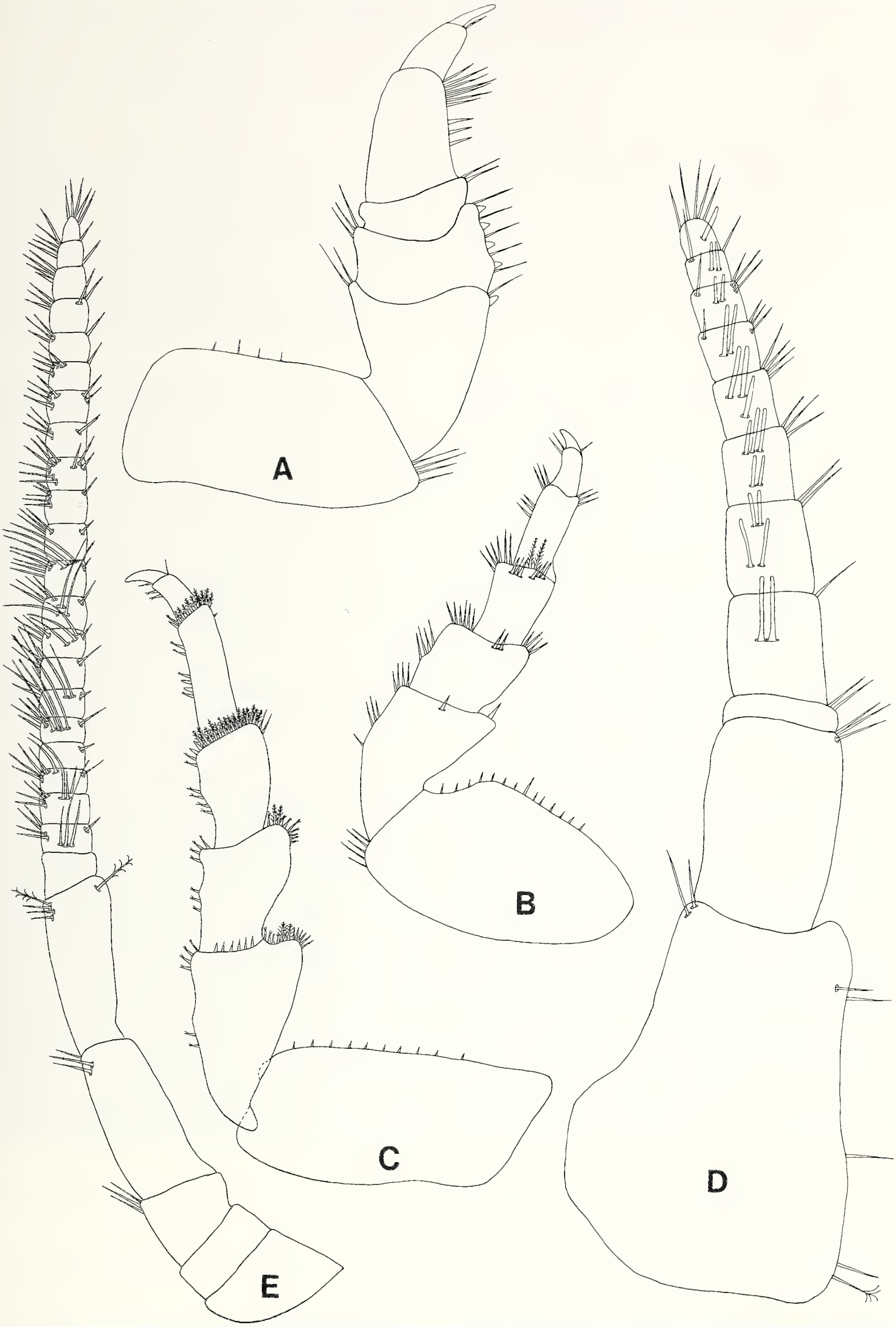


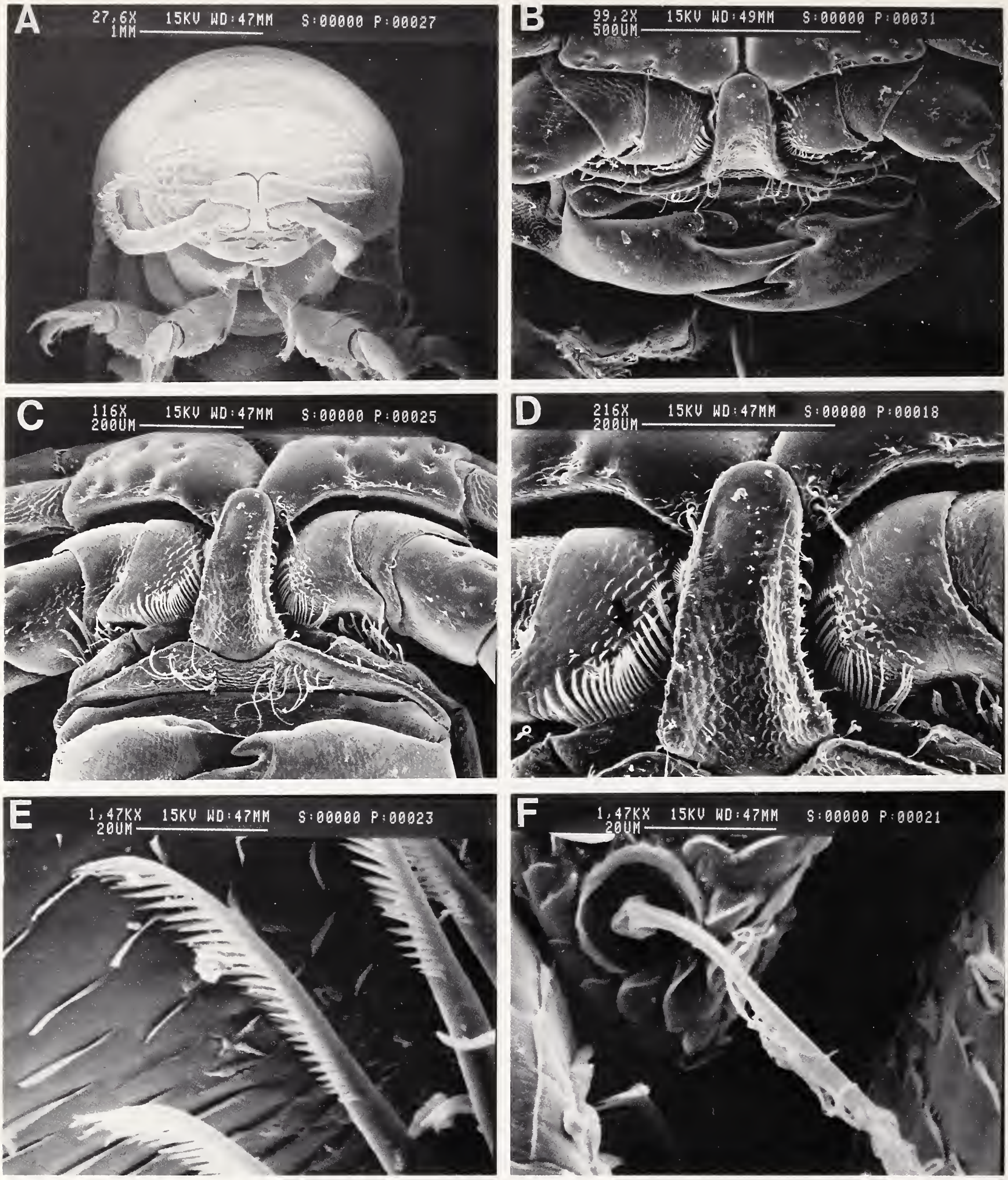
Figure 19. *Excorallana bruscai,* AHF holotype #6611: **A,** pereopod I; **B,** pereopod IV; **C,** pereopod VII; **D,** antennule; and **E,** antenna.

7) *Excorallana truncata* (Richardson, 1899a):825, figure 4; Nierstrasz, 1931:177; Lemos de Castro, 1960:61, 1964:4; Monod, 1969:50; Carvacho and Yanez, 1971:130; Delaney, 1982: 273, 1984:18.

*Corallana truncata* Richardson, 1899a:825, 1899b:165, 1900a:217, 1901:517; Nierstrasz, 1917:101.

*Exocorallana truncata* Richardson, 1905:145 (*lapsus calami*).

*Excorallana kathyae* Menzies, 1962b:345; Monod, 1969:50.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200UM
D
216X 15KV WD:47MM S:00000 P:00018
200UM
E
1.47KX 15KV WD:47MM S:00000 P:00023
20UM
F
1.47KX 15KV WD:47MM S:00000 P:00021
20UM

**Figure 20.** Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: **A**, anterior view of cephalon; **B**, detail of cephalon showing frontal lamina and mandibles; **C**, detail of frontal lamina and mandibles; **D**, frontal lamina; **E**, plumose seta at base of antenna (in D); and **F**, seta in pit on antennule peduncle (in D).

**DISTRIBUTION.** Point Conception, California to Galapagos Islands.

8) *Excorallana berbicensis* Boone, 1919:594, plate 92, figure 1; Van Name, 1925:471; Lemos de Castro, 1960:61, 1964:5; Monod, 1969:50; Carvacho, 1977a:12; Delaney, 1984:3.
*Excorallana barbicensis* Carvacho and Yanez, 1971:129 (*lapsus calami*).

**DISTRIBUTION.** Caribbean.

9) *Excorallana longicornis* Lemos de Castro, 1960: 61, figures 1–10, 1964:5; Monod, 1969:50; Carvacho and Yanez, 1971:130; Delaney, 1984:3.

**DISTRIBUTION.** Brazil.

10) *Excorallana mexicana* Richardson, 1905:142, figures 122, 123; Lemos de Castro, 1960:61, 1964:4; Monod, 1969:48; Carvacho and Yanez, 1971:129; Menzies and Kruczynski, 1983:72; Delaney, 1984:3.
*Exocorallana mexicana* Richardson, 1905:142 (*lapsus calami*).
*Corallana mexicana* Nierstrasz, 1917:101.

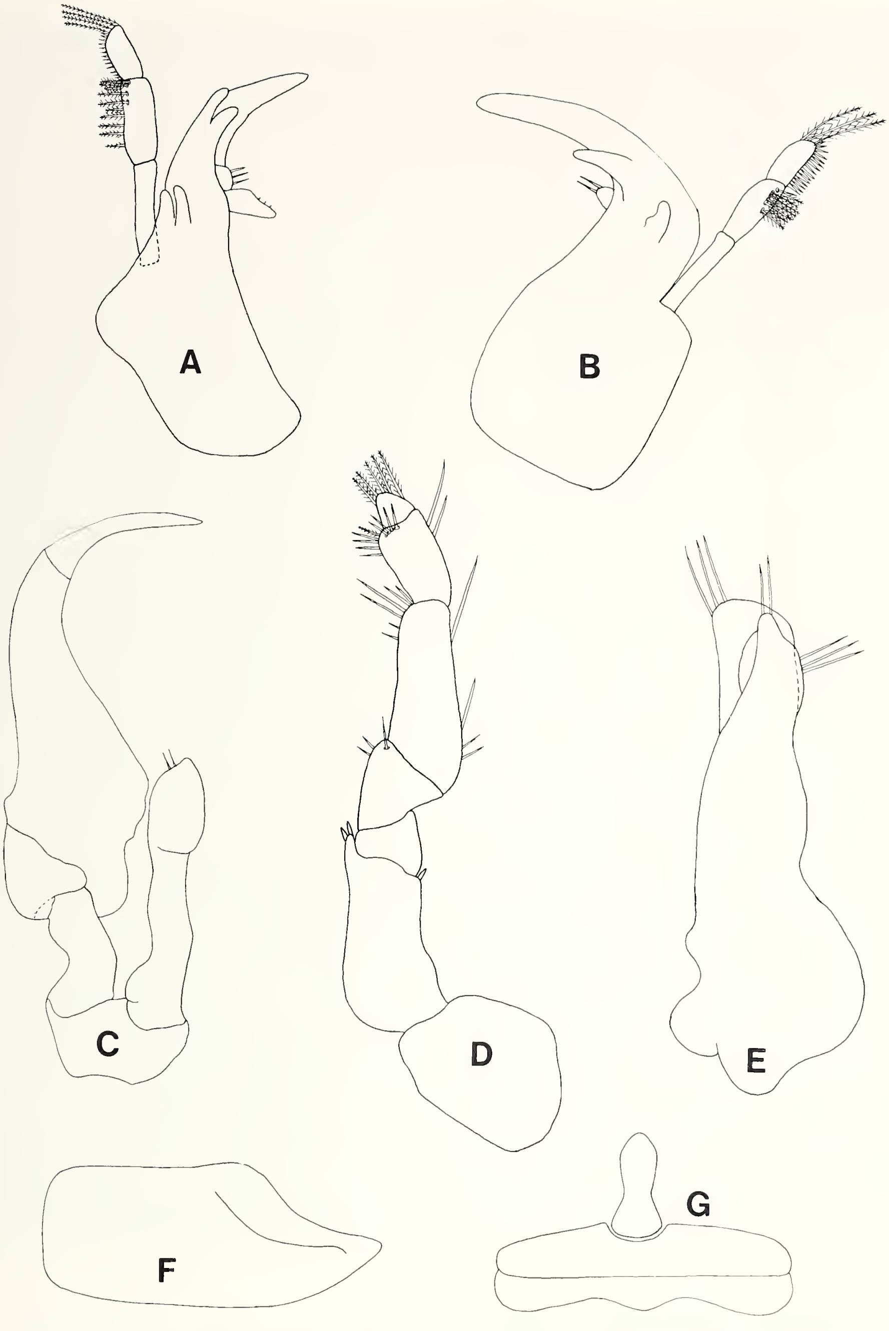


Figure 21. *Excorallana bruscai,* AHF holotype #6611: **A,** left mandible; **B,** right mandible; **C,** maxillule; **D,** maxilliped; **E,** maxilla; **F,** coxa VII; and **G,** frontal lamina, clypeus, and labrum.

**DISTRIBUTION.** Gulf of Mexico and Caribbean.

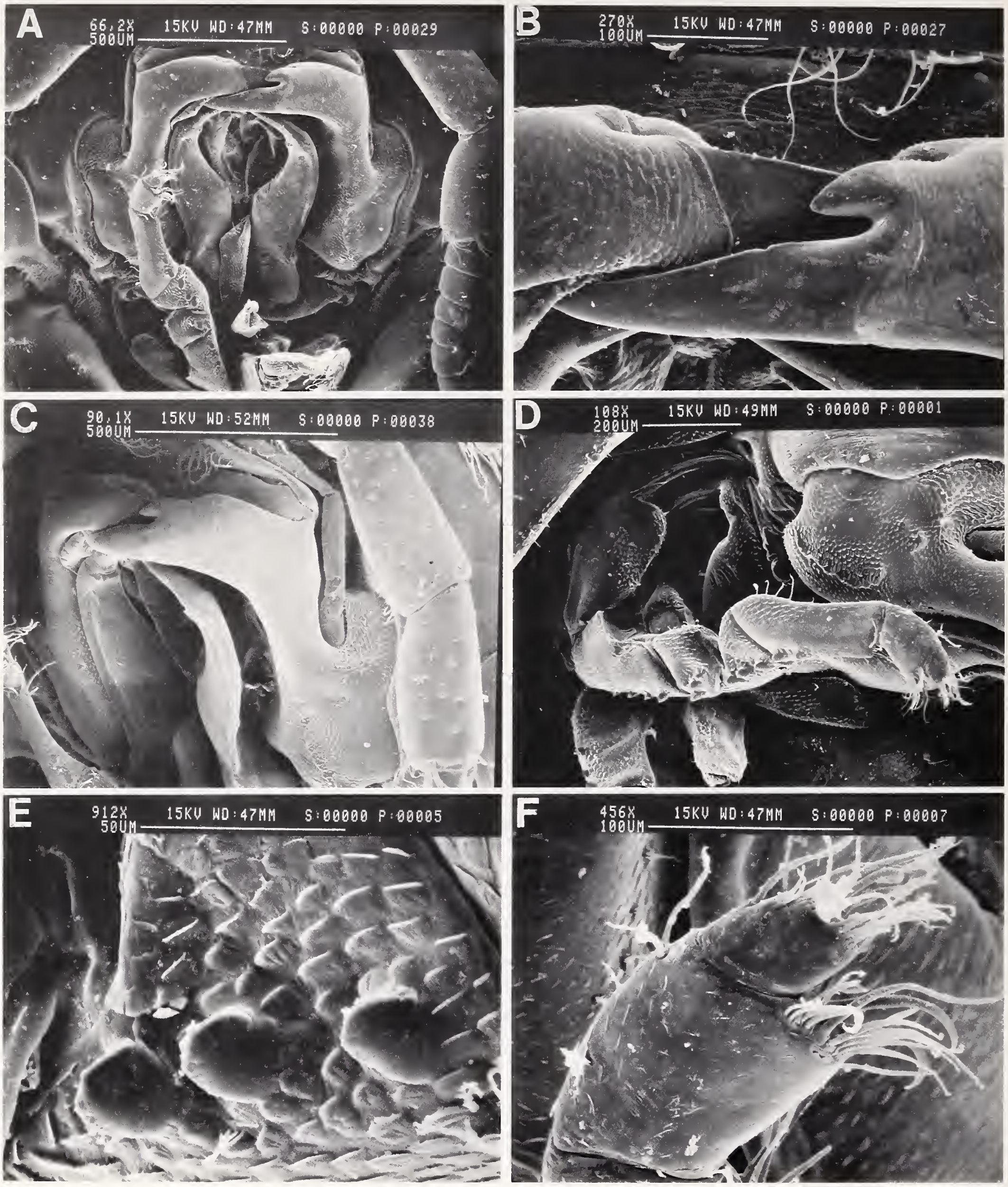
11) *Excorallana oculata* (Hansen, 1890):386, table VII, figures 6a, b; Boone, 1921:93; Lemos de Castro, 1960:61, 1964:5; Monod, 1969:50; Carvacho and Yanez, 1971:129; Delaney, 1984:3.

*Corallana oculata* Hansen, 1890:386; Richardson, 1901:517; Nierstrasz, 1917:101.

*Exocorallana oculata* Richardson, 1905:152 (*lapsus calami*).

**DISTRIBUTION.** Caribbean, Brazil, and West Africa (Isle Annobon).

12) *Excorallana quadricornis* (Hansen, 1890):382, table VII, figure 2; Lemos de Castro, 1960:61, 1964:1; Monod, 1969:50; Carvacho and Yanez, 1971:129; Carvacho, 1977a:11; Delaney, 1984:3.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B
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C
90.1X 500UM 15KV WD:52MM S:00000 P:00038
D
108X 200UM 15KV WD:49MM S:00000 P:00001
E
912X 50UM 15KV WD:47MM S:00000 P:00005
F
456X 100UM 15KV WD:47MM S:00000 P:00007

**Figure 22.** Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: **A,** buccal field; **B,** mandible incisors; **C,** lateral view of mandible and maxillule; **D,** maxilliped; **E,** tubercles on second article of maxilliped palp; and **F,** distal articles of maxilliped palp.

*Corallana quadricornis* Hansen, 1890:382; Richardson, 1901:517, 1902:290; Nierstrasz, 1917:101.

*Exocorallana quadricornis* Richardson, 1905: 144, 1912:188 (*lapsus calami*).

**DISTRIBUTION.** Caribbean and Brazil.

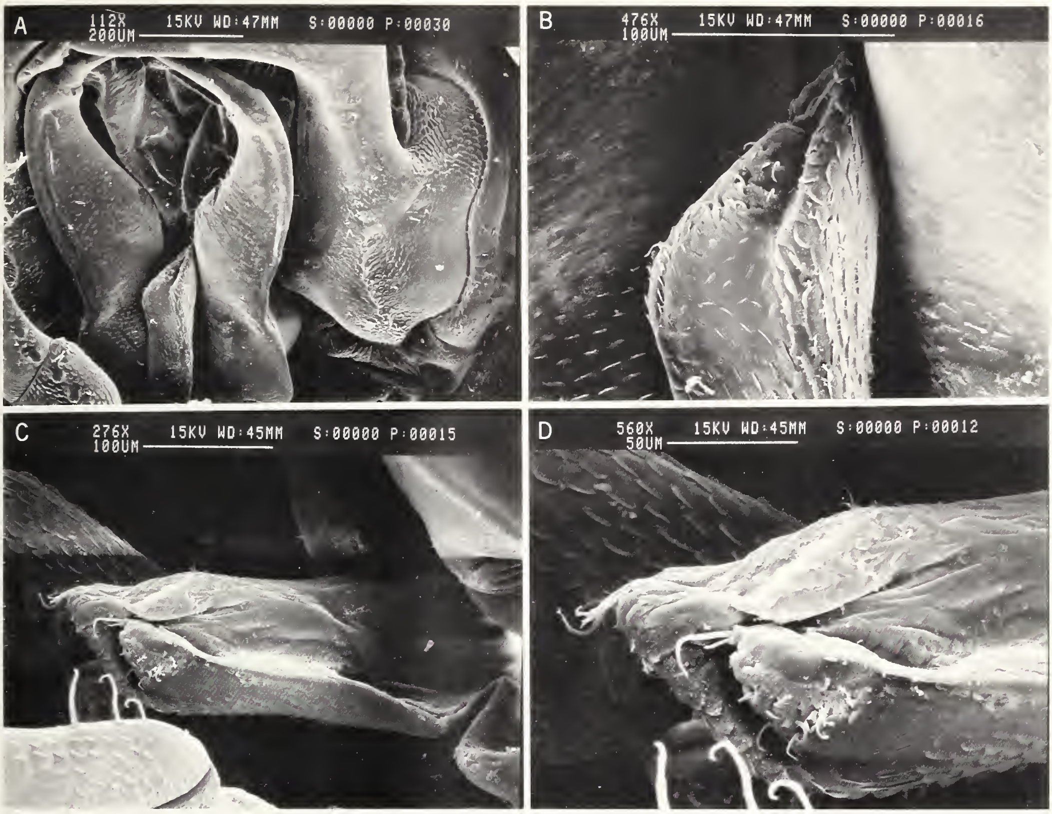
13) *Excorallana sexticornis* (Richardson, 1901): 518, figure 9; Lemos de Castro, 1960:61, 1964: 5; Monod, 1969:50; Carvacho and Yanez, 1971:129; Delaney, 1984:3.

*Corallana sexticornis* Richardson, 1901:518; Nierstrasz, 1917:101.

*Exocorallana sexticornis* Richardson, 1905:143 (*lapsus calami*).

**DISTRIBUTION.** Caribbean.

14) *Excorallana warmingii* (Hansen, 1890):387, table VII, figures 7a–f; Lemos de Castro, 1960: 61, 1964:5; Monod, 1969:50; Carvacho and Yanez, 1971:130; Schultz, 1979:224; Delaney, 1984:3.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B
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100UM
C
276X 15KV WD:45MM S:00000 P:00015
100UM
D
560X 15KV WD:45MM S:00000 P:00012
50UM

**Figure 23.** Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: **A**, ventral view of maxilla, maxillule, and mandible base; **B**, maxilla apex; **C**, dorsal view of maxilla; and **D**, detail of maxilla apex (in C).

*Corallana warmingii* Hansen, 1890:387; Richardson, 1901:517; Nierstrasz, 1917:101.
*Exocorallana warmingii* Richardson, 1905:154 (*lapsus calami*).

**DISTRIBUTION.** Caribbean.

15) *Excorallana fissicauda* (Hansen, 1890):385, table VII, figures 5a–d; Lemos de Castro, 1960: 61, 1964:5; Monod, 1969:48; Carvacho and Yanez, 1971:129; Delaney, 1984:3.
*Corallana fissicauda* Hansen, 1890:385; Richardson, 1901:517; Nierstrasz, 1917:101.
*Exocorallana fissicauda* Richardson, 1905:150 (*lapsus calami*).

**DISTRIBUTION.** Caribbean.

16) *Excorallana angusta* Lemos de Castro, 1960: 63, figures 11–18, 1964:5; Monod, 1969:50; Carvacho anad Yanez, 1971:130; Delaney, 1984:3.

**DISTRIBUTION.** Brazil.

17) *Excorallana richardsonae* Lemos de Castro, 1960:64, figures 19–27, 1964:4; Monod, 1969: 50 (emendation).
*Excorallana richardsoni* Lemos de Castro, 1960: 64, 1964:4; Carvacho and Yanez, 1971:130; Delaney, 1984:3 (*lapsus calami*).

**DISTRIBUTION.** Brazil.

18) *Excorallana costata* Lemos de Castro, 1960: 66, figures 28–37, 1964:4; Monod, 1969:50; Carvacho and Yanez, 1971:130; Delaney, 1984:3.

**DISTRIBUTION.** Brazil.

19) *Excorallana meridionalis* Carvacho and Yanez, 1971:129, plates I, II; Carvacho, 1977b:27; Delaney, 1984:3.

**DISTRIBUTION.** Chile.

20) *Excorallana stebbingi* Lemos de Castro and Lima, 1976:75, figures 1–14.

**DISTRIBUTION.** Brazil.

## REMARKS

Delaney (1984) reviewed the status of this genus and noted the need for a thorough revision. Previously, the most comprehensive treatments of this group have been Richardson (1905), Lemos de Castro (1960, 1964), Monod (1969), and Carvacho and Yanez (1971).

Sexual dimorphism in dorsal ornamentation is common. In many species males possess dorsal tu-

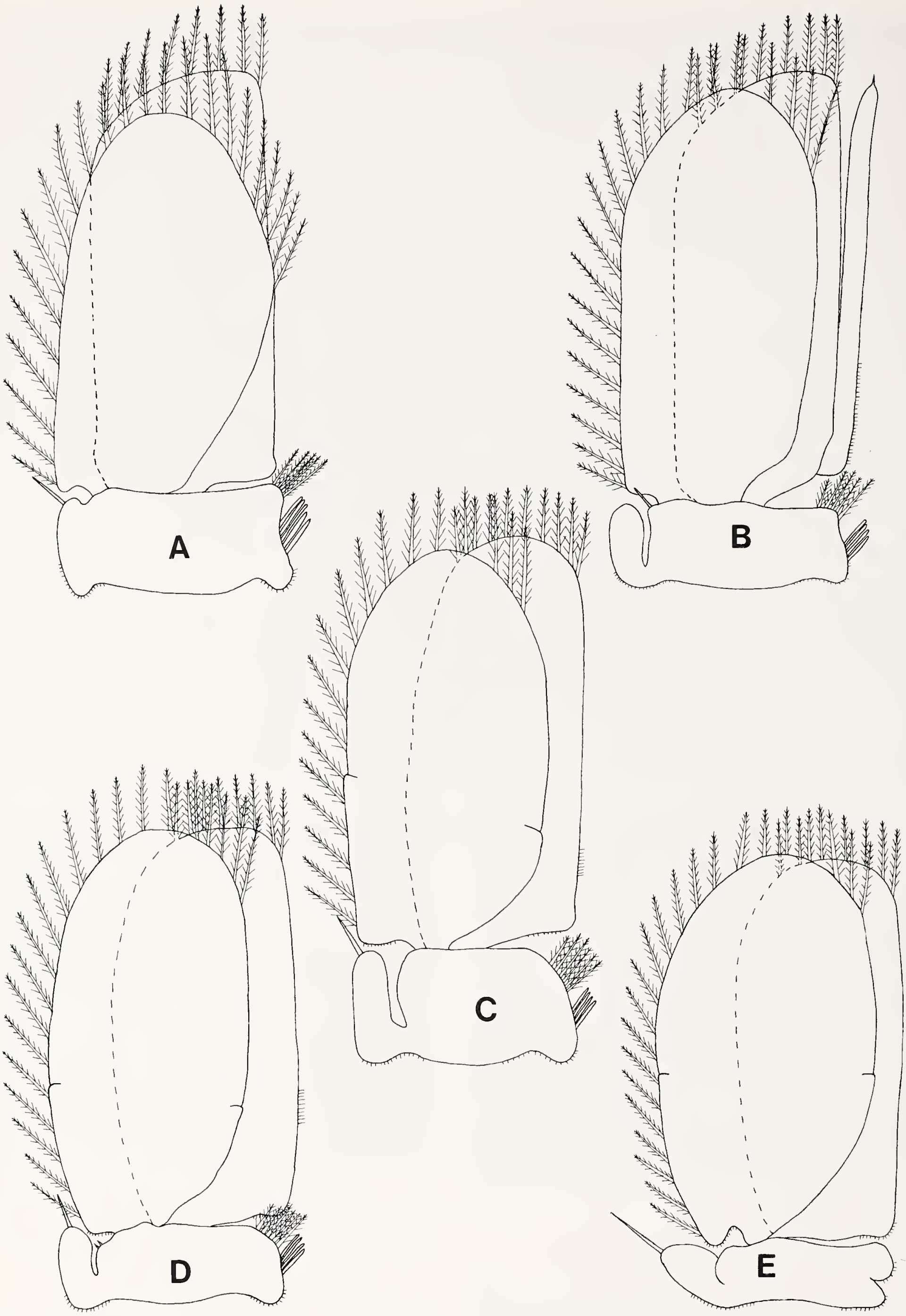


**Figure 24.** *Excorallana bruscai,* AHF holotype #6611: **A,** pleopod 1; **B,** pleopod 2; **C,** pleopod 3; **D,** pleopod 4; and **E,** pleopod 5.

bercles or "horns" on the cephalon and pereonite I, but in females these are usually lacking, or if present are generally reduced in size or number. Size of dorsal ornamentation may also be related to the age and maturity of the isopod.

Based upon examination of type-specimens of *Excorallana acuticauda* and *E. antillensis,* the latter is herein made a junior synonym of *E. acuticauda. Excorallana subtilis* is very similar to *E. acuticauda* and *E. richardsonae,* differing primarily in degree of dorsal setosity and the tuberculation of the pleon; herein I maintain it as a distinct species, but more specimens are needed to ascertain its true status.

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

*Excorallana* is the largest genus in the family Corallanidae. The genus is primarily confined to the New World tropics, between the latitudes of 40°N and 40°S (Fig. 25). One species, *Excorallana oculata,* has been collected from tropical west Africa. A number of Atlantic-Pacific "analog" or geminate species pairs exist, supporting the concept of a generalized trans-isthmian oceanic track connecting the eastern Pacific and Caribbean prior to the formation of the Panamanian isthmus (Woodring, 1966; Croizat et al., 1974).

*Excorallana* species probably emerge from cryptic habitats to temporarily parasitize fish or to prey on microcrustaceans and other invertebrates. Species in this group have been collected from depths of 183 m to the intertidal zone, and from a variety of habitats including coral reefs, limestone conglomerate (coquina) reefs, mangrove areas, andesite rock, and sand beaches. They have been collected as "commensals" of ascidians, calcareous sponges, and tube-building snails, as well as temporary parasites (or micropredators) of numerous fish species.

Menzies and Kruczynski (1983) presented evidence that some species of *Excorallana, Alcirona,* and *Lanocira* may partition their habitats by depth range in the Gulf of Mexico. Delaney (1984) found *E. bruscai* to exhibit an aggregated dispersion pattern as a cryptofaunal inhabitant of a limestone conglomerate reef at Puerto Penasco, Sonora, Mexico. The dispersion index was greatest in the upper (0′ to +2′) intertidal zone during January, but greatest in the lower zone (0′ to −2′) during April. This may indicate that some seasonal movement within the intertidal zone occurs in this species, perhaps related to the occurrence of gravid females (which were only found in April). *Excorallana tricornis occidentalis* is part of the demersal zooplankton at Isla Cano, Costa Rica, exhibiting definite nocturnal migration from the benthos to the water column. This species may prey on microcrustaceans such as mysids (Guzman et al., 1988). See Delaney (1984) and the Material Examined section of this study for extensive habitat and host data for other species in this genus.

## Genus *Lanocira* Hansen, 1890

*Lanocira* Hansen, 1890:395; Stebbing, 1893:315, 1904b:706, 1905:19, 1909:217; Moore, 1902:170; Richardson, 1910:8; Barnard, 1914:359, 1920:354, 1940:491, 1955:61; Nierstrasz, 1917:102, 1931: 167; Monod, 1933:187; Pillai, 1954:7, 1967:272; Kensley, 1978:75; Bruce, 1980:315; Jones, 1982: 65; Bruce et al., 1982:464; Delaney and Brusca, 1985:728.

*Nalicora* Moore, 1902:169; Richardson, 1905:164; Jones, 1982:72; Bruce et al., 1982:464; Menzies and Kruczynski, 1983:77.

*Corilana* Kossman, 1880:115; Nierstrasz, 1917:102, 1931:172; Monod, 1933:190; Bruce et al., 1982: 464.

### MATERIAL EXAMINED

*Lanocira kroyeri:* 1) Brazil, Rio de Janiero, ZMUC holotype, 1 fe., 3.8 mm. *Lanocira rotundicauda:* 1) Indonesia, Jakarta Bay, Seribu Islands, Pulau Edam, Java, CAS No. 025372, Quad. #R-082766, "sand and coral bottom," 2 fe., 6.6 and 6.6 mm, and 3 mancas, all 2.4 mm. *Lanocira rapax:* 1) Gulf of Mexico, off Florida, USNM 11775, *Albatross,* Sta. 2369-74, 29°16′30″N, 85°32′W, depth 47 m, 34 spec.; 2) Gulf of Mexico, between delta of Mississippi River and Cedar Keys, Florida, USNM 46344, Sta. 2369-74, "out of USNM 39405," 5 fe. (gravid); 3) Puerto Rico, Mayaguez, north of Punta del Algarrobo, USNM 44279, coll. U.S. Fish Commission Porto Rico Expedition, 1898–1899, *Fish Hawk,* Sta. 138, 1 ma.; 4) West Indies, USNM Acc. No. 208263, Sta. 55-56, 1 fe. *Lanocira gardineri:* 1) Hong Kong, Ninepino, North Reef, AM No. P31524, "from sponge, 15 m," 1 fe., 6.4 mm; 2) Red Sea, Suez, ZMHUB No. 1314, 3 fe., 4.5, 5.2, and 5.8 mm, 5 ma., 3.4 (fragment), 4.0, 4.4, 4.9, and 5.6 mm, and 10 embryos, 1.0–1.25 mm; 3) Persian Gulf, Iraq, Khor Abdullah, near Um Quasor, ZMHUB, "11 a.m., sublittoral, depth 2m, water temp. = 25°C, taken with dredge," 1 fe., 6.8 mm, and 2 ma., 6.4 and 7.4 mm; 4) Philippines, Corregidor Straits, USNM 40956, R/V *Albatross,* Sta. D5108, depth 23 m, 5 fe. and 2 ma.; 5) West Pacific Ocean, Eniwetok Atoll, Runit Island, USNM Acc. No. 172586, "intertidal," 2 ma.; 6) Madagascar, Nossi-Be, Ankifi Beach, IIOE Program, SOSC, J. Rudloe, Ref. 54, Sta. JR-36, 13°31′S, 48°32′E, depth 0–0.2 m, 2 ma. and 4 mancas; 7) Madagascar, Nossi-Be, Ankifi Beach, IIOE Program, SOSC, J. Rudloe, Sta. JR-22, 13°31′S, 48°32″E, depth 0–0.2 m, 1 ma. and 1 manca; 8) Madagascar, Nossi-Be, Ankifi Beach, IIOE Program, SOSC, J. Rudloe, Sta. JR-19/JR-4, 2 ma. and 3 mancas; 9) Mozambique, Ponta da Barra Ralsa, USNM 40956, IIOE Program, R/V *Anton Bruun* Cruise 8, Sta. 400C, "GMST gear," 20°30′S, 35°43′E, depth 62 m, 2 fe., 3 ma., and 3 mancas; 10) Philippine Islands, USNM, R/V *Albatross,* No. 2369-74, 1 fe. *Lanocira zeylanica:* 1) West Pacific Ocean, Bikini Island, USNM Acc. No. 176603, "from boat cradle, anchored in lagoon," 1 fe.; 2) West Pacific, Japtan Island, USNM Acc. No. 197874, H.S. Ladd, Sta. 1523, "seaward," 1 fe.; 3) East Pacific, Juan Fernandez Islands, Father Bay, USNM Acc. No. 93322, "given to S. Durand by fisherman," depth 54 m, 2 fe. and 1 ma.; 4) East Pacific, Juan Fernandez Islands, Santa Clara Island, USNM Acc. No. 93322, "collected from an antipatharian," 1 fe.; 5) Juan Fernandez Islands, Santa Clara Island, West Bay, USNM Acc. No. 93322, 36–45 m, 1 ma.; 6) Juan Fernandez Islands, Acla. Vaguena, USNM Acc. No. 93322, depth 32 m, 1 fe. and 2 ma.; 7) Juan Fernandez Islands, Carbojal Bay, USNM Acc. No. 93322, "dredged at 27–36

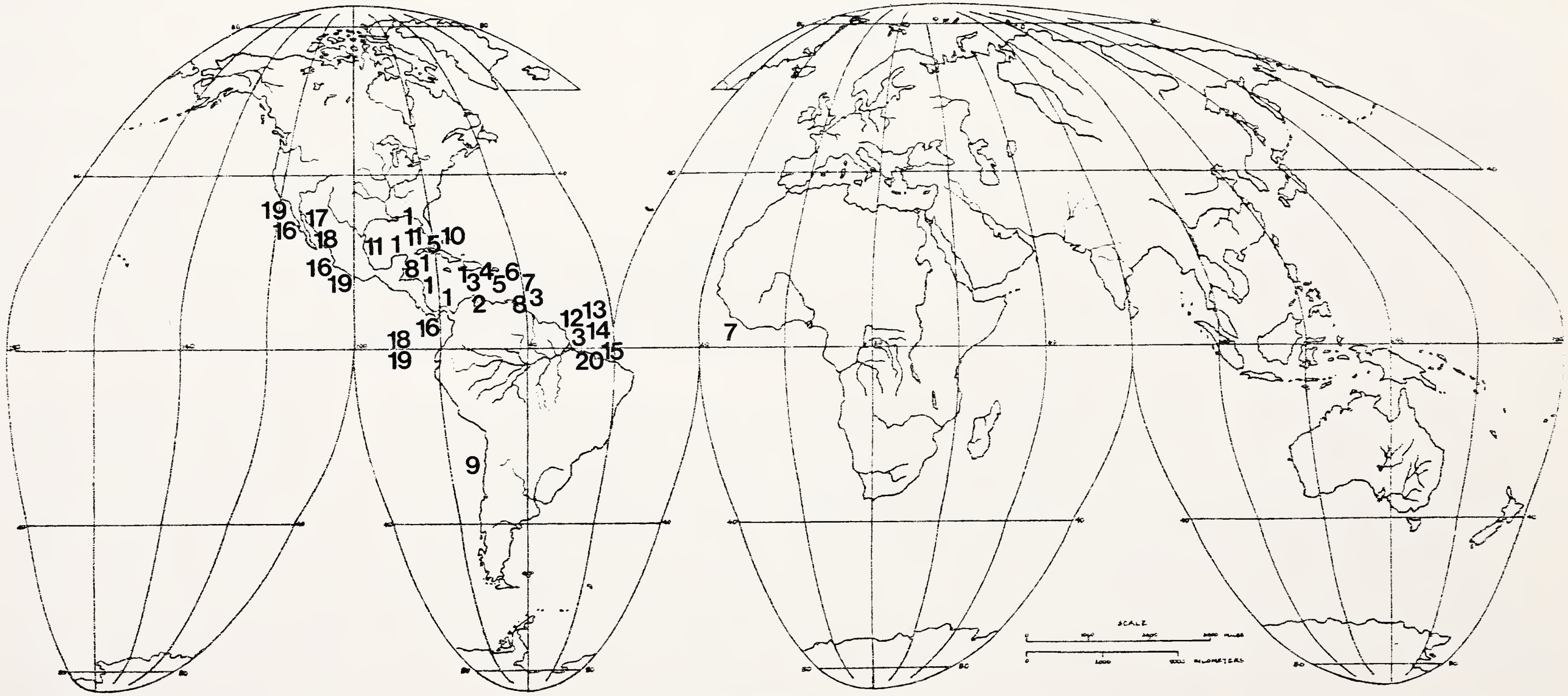


**Figure 25.** Distribution of *Excorallana* species; species numbers are: 1, *E. tricornis tricornis;* 2, *E. berbicensis;* 3, *E. quadricornis;* 4, *E. subtilis;* 5, *E. acuticauda;* 6, *E. fissicauda;* 7, *E. oculata;* 8, *E. warmingii;* 9, *E. meridionalis;* 10, *E. sexticornis;* 11, *E. mexicana;* 12, *E. longicornis;* 13, *E. costata;* 14, *E. angusta;* 15, *E. richardsonae;* 16, *E. tricornis occidentalis;* 17, *E. bruscai;* 18, *E. houstoni;* 19, *E. truncata;* and 20, *E. stebbingi.*

m," 3 spec.; 8) Juan Fernandez Islands, Santa Clara Islands, off West Bay, USNM Acc. No. 93322, "from fisherman," depth 45 m, 23 spec.; 9) Indian Ocean, Mahe' Island, small baylet immediately south of north point on west side of island, just off the Fairhaven Hotel, USNM Acc. No. 276969, IIOE Program, Sta. F-35, depth 8–11 m, 1 ma.; 10) South Pacific Ocean, SEBOP Program, SOSC, coll. R/V *Anton Bruun* Cruise 12, Sta. MV-65IV54, 33°38'S, 78°45'W, "otter trawl/benthic," 1 fe., 1 ma., 1 juvenile, and 4 mancas; 11) East Pacific Ocean, USNM, R/V *Anton Bruun* Cruise 12, Sta. 65256, Marsden Square, No. 415-2, "diving gear," 1 ma.; 12) Indian Ocean, Seychelle Islands, Faon Island, off south shore, USNM Acc. No. 276969, IIOE Program, Sta. F-11, depth 11–15 m, 1 fe. *Lanocira latifrons:* 1) Mozambique, Ponta da Barra Ralsa, USNM 40956, IIOE Program, R/V *Anton Bruun* Cruise 8, Sta. 400C, "GMST gear," 20°30'S, 35°43'E, depth 62 m, 1 ma.; 2) Red Sea, Suez, ZMHUB No. 13124, "from the umbrella of *Cassiopea andromeda* (Scyphozoa)," 1 fe., 4.6 mm (gravid with 5 embryos, 0.7–0.8 mm).

### DIAGNOSIS

Antennule peduncle 2-articulate; basal article of peduncle narrow, not expanded. Frontal lamina narrow, pentagonal; clypeus broad, short; labrum small. Mandible with broad base, slender trunk and apex, and short incisor, with row of short recurved spines or dentate processes on lateral margin behind incisor; molar process usually small or absent, occasionally moderately sized, lacinia mobilis small or absent. Maxillule lateral lobe forming single large falcate spine; medial lobe simple, apically blunt. Maxilla 3- or 4-articulate, apical article sublinear, elongate, with two long apical setae. Maxilliped without endite; basis not elongate; palp broad, always 5-articulate, middle article not elongate. Anterior pereopods usually without serrate dactyli and propodi (except in *L. zeylanica* as figured by Monod, 1933:184); carpi not produced as in *Tachaea.*

### ADDITIONAL DESCRIPTION

Corallanidae with well-developed eyes at anterolateral margin of cephalon. Dorsum often with tubercles or setae (Fig. 1E). Dorsum of some species densely covered with cuticular sensillae arising from pits or from globate sockets (Figs. 26C, E–F, 27). Antennule peduncle basal article not enlarged (Fig. 28A). Antenna peduncle articles 4 and 5 elongate (Fig. 26B). Clypeus much smaller relative to labrum than in *Alcirona* and *Argathona;* labrum small, but often conceals incisor of mandible (Figs. 26D, 28E). Mandible palp inserted near mandible base; 3-articulate, middle article longest, middle and distal articles with simple marginal setae, middle article with plumose setae (Figs. 28B, 29E, F). Maxillule lateral (outer) lobe forming single large falcate spine; medial margin with knoblike process in *L. rapax;* medial (inner) lobe simple with 0–2 small setae (Figs. 28H, 29D). Maxilla apical article sublinear, elongate, with 2 long apical setae (Figs. 28F, G, 29C). Maxilliped palp apical, lateral and medial margins with simple and plumose setae (Figs. 28C, 29A, B). Pereopods I–III subprehensile, meri with stout spines on posteromedial margins (Figs. 28D, 30A, 31A, B). Pereopods IV–VII longer, ambulatory, with simple setae and stout spines on posteromedial margins (Figs. 30B, C, 31C, D). Pleopod peduncles broader than long, with 3–5 coupling spines and groups of proximal plumose setae on medial margins, and with simple spine on lateral margins (Figs. 30D–H, 31E, F). Pleopod exopods broader and with more plumose marginal setae than endopods. Endopod of pleopod 5 naked, proximal medial margin produced, lobelike (Fig. 30H). Male pleopod 2 with rodlike appendix maculina, with simple apex, arising from proximal medial margin of endopod (Fig. 30E).

### TYPE SPECIES

*Lanocira kroyeri* Hansen, 1890:396, plate VIII, figures 3a–l, by monotypy.

### DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

1) *Lanocira kroyeri* Hansen, 1890:396, plate VIII, figures 3a–l; Stebbing, 1893:315, 1904b:707, 1905:20, 1909:218; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Jones, 1982:73.

**DISTRIBUTION.** Rio de Janeiro, Brazil.

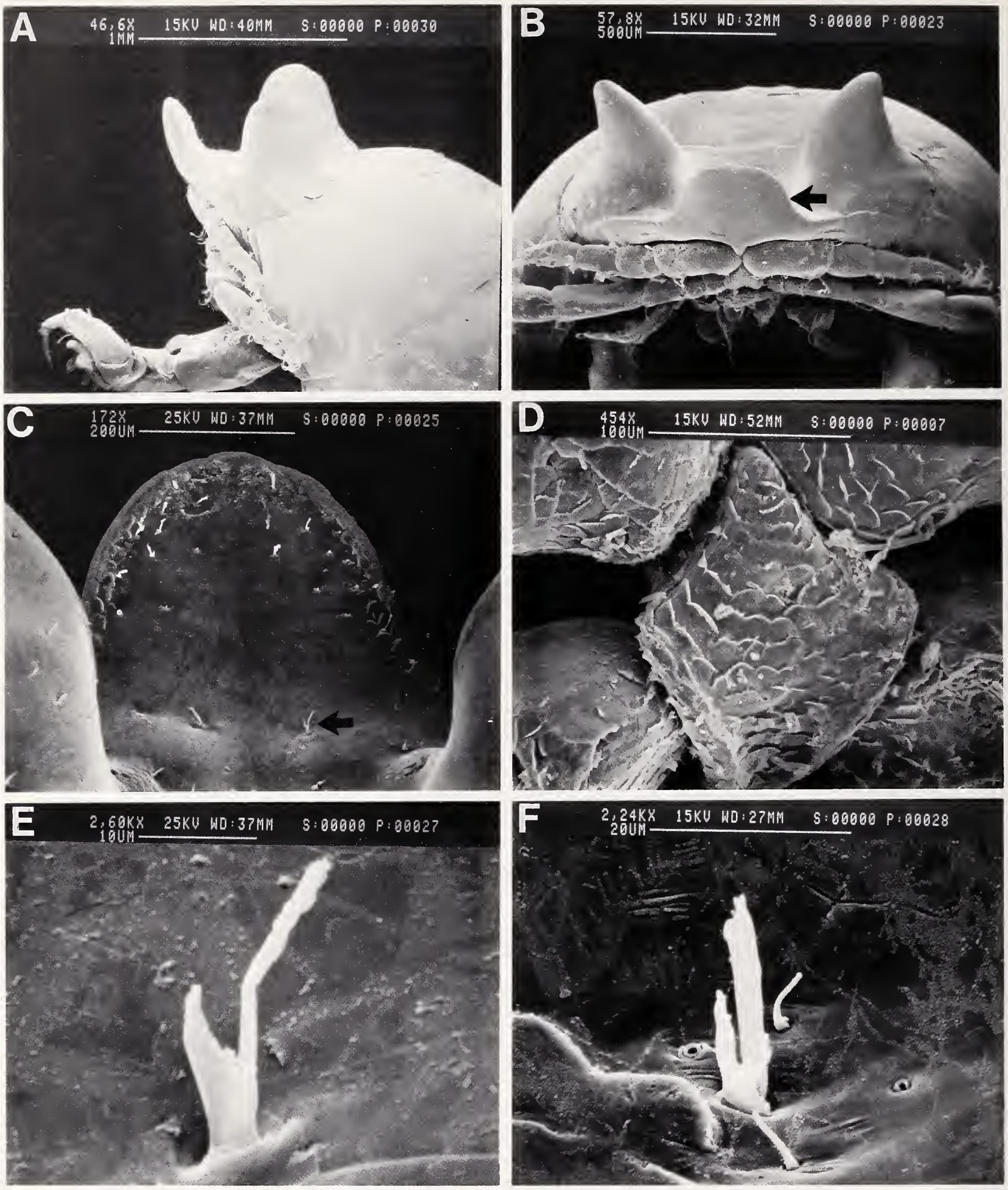
2) *Lanocira rapax* (Moore, 1902):169, plate 9, figures 11–22; Richardson, 1905:164; Nierstrasz, 1917:102; Jones, 1982:72.
*Nalicora rapax* Moore, 1902:169; Richardson, 1905:164; Menzies and Kruczynski, 1983:77.
*Excorallana rapax* Schultz, 1969:211; Menzies and Kruczynski, 1983:77.

**DISTRIBUTION.** Puerto Rico, Florida, and Gulf of Mexico.

3) *Lanocira gardineri* Stebbing, 1904b:706, plate LI-a, 1905:19, 1909:218; Richardson, 1910:9; Barnard, 1914:359, 1920:354, 1940:491, 1955:61; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Pillai, 1954:7, 1967:274; Kensley, 1978:75; Bruce, 1980:316; Jones, 1982:72.
*Lanocira capensis* Barnard, 1914:359, plate 31A, 1920:354; Nierstrasz, 1931:169; Monod, 1933:188; Bruce, 1980:316; Jones, 1982:72.

**DISTRIBUTION.** Maldives, South Africa, Philippines, India, Kenya, Sri Lanka, Hong Kong, Persian Gulf, Mozambique, Madagascar, and Eniwetok Atoll.

4) *Lanocira rotundicauda* Stebbing, 1904b:707, plate L-a, 1905:19; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Pillai, 1967:272; Bruce, 1980:316; Jones, 1982:74.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1MM
B
57.8X 15KV WD:32MM S:00000 P:00023
500UM
C
172X 25KV WD:37MM S:00000 P:00025
200UM
D
454X 15KV WD:52MM S:00000 P:00007
100UM
E
2.60KX 25KV WD:37MM S:00000 P:00027
10UM
F
2.24KX 15KV WD:27MM S:00000 P:00028
20UM

**Figure 26.** Scanning electron micrographs of *Lanocira gardineri*, USNM 40956: **A,** lateral view of cephalon and pereonite I; **B,** anterior view of cephalon and rostral process; **C,** posterior view of rostral process; **D,** frontal lamina; **E,** cuticular sensillum on rostrum (arrow in C); and **F,** cuticular sensillae on posterior cephalon.

DISTRIBUTION. Maldives, Sri Lanka, and Indonesia.

5) *Lanocira zeylanica* Stebbing, 1905:19, plate 5b, 1909:218; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Barnard, 1955:61; Pillai, 1967:272.

*Lanocira zeylandica* Jones, 1982:72 (*lapsus calami*).

*Lanocira hirsuta* Nordenstam, 1930:541.

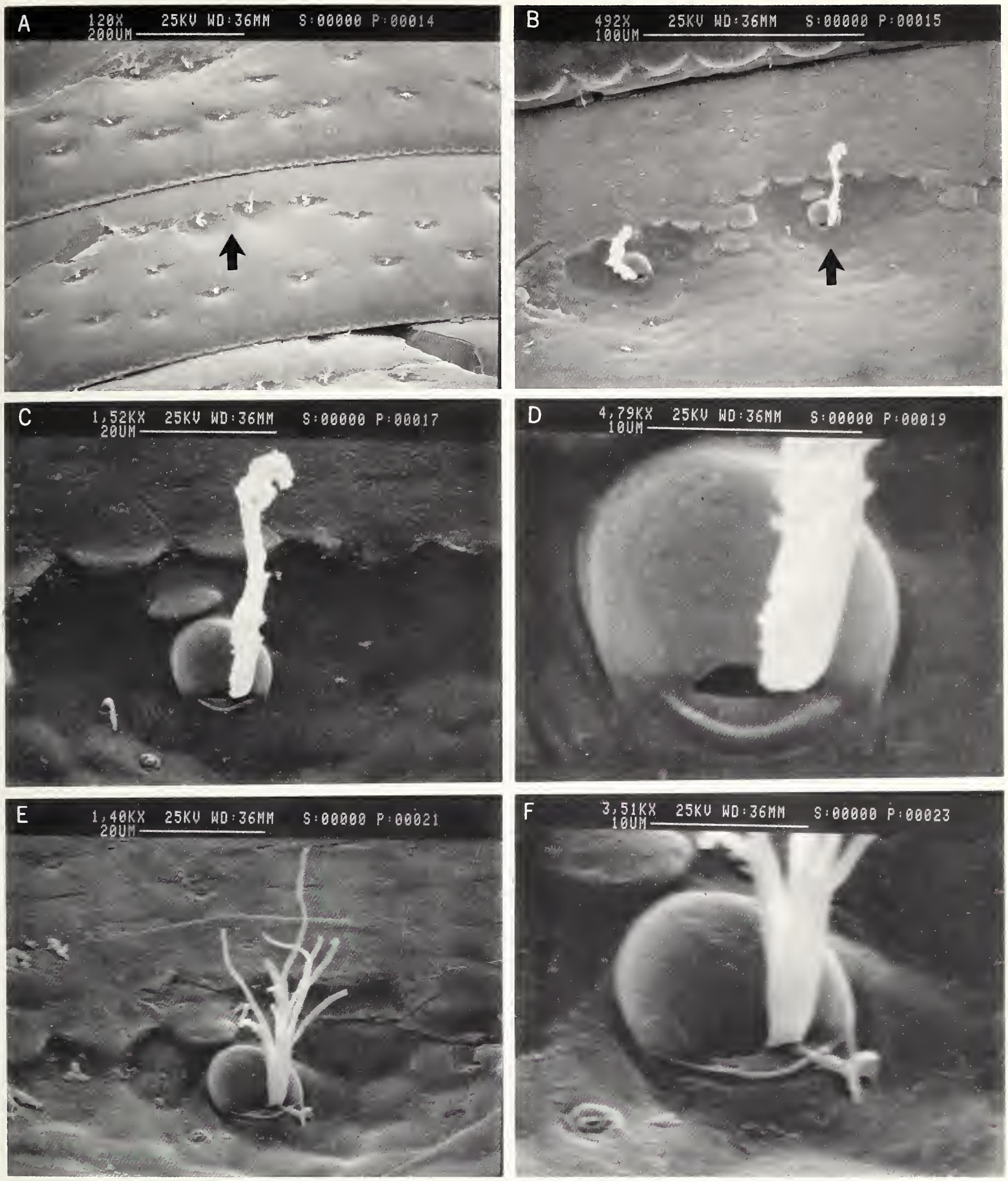
DISTRIBUTION. Sri Lanka, Tanzania, Kenya, Red Sea, Juan Fernandez Islands, Easter Island, Bikini Island, and Japtan Island.

6) *Lanocira latifrons* Stebbing, 1909:217; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Barnard, 1955:61; Kensley, 1978:75; Jones, 1982:72.

DISTRIBUTION. South Africa, Mozambique, and Red Sea.

7) *Lanocira glabra* Jones, 1982:65.

DISTRIBUTION. Watamu, Kenya.


A
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B
492X 25KV WD:36MM S:00000 P:00015
100UM
C
1,52KX 25KV WD:36MM S:00000 P:00017
20UM
D
4,79KX 25KV WD:36MM S:00000 P:00019
10UM
E
1,40KX 25KV WD:36MM S:00000 P:00021
20UM
F
3,51KX 25KV WD:36MM S:00000 P:00023
10UM

**Figure 27.** Scanning electron micrographs of *Lanocira gardineri*, USNM 40956: **A**, dorsal view of pereonite III; **B**, cuticular structures on pereonite III; C, one cuticular structure; **D**, detail of cuticular structure (in C); **E**, pleonal cuticular structure; and **F**, detail of pleonal cuticular structure (in E).

8) *Lanocira anasicula* Jones, 1982:68.

**DISTRIBUTION.** Watamu, Kenya.

## REMARKS

The genus *Lanocira* was erected by H.J. Hansen in 1890 for his new species *Lanocira kroyeri*. Kossman (1880) proposed the new genus and species *Corilana erythraea;* this poorly defined genus was regarded as *genus et species inquirenda* by Monod (1933) and regarded as closest to *Lanocira* by Bruce et al. (1982). Moore (1902) erected the genus *Nalicora* to house her new species *Nalicora rapax,* which she placed in the Alcironidae. Jones (1982) synonymized *Nalicora* with *Lanocira.*

The maxilla of *Lanocira* is 3- or 4-articulate, with a sublinear, elongate apical article and 2 long apical setae—a unique character state in the Corallanidae. The maxilla has been figured as 4-articulate by Hansen (1890), Moore (1902), Stebbing (1904a, b), and Richardson (1905), and as 3-articulate by Stebbing (1905), Barnard (1914), Monod (1933), and Jones

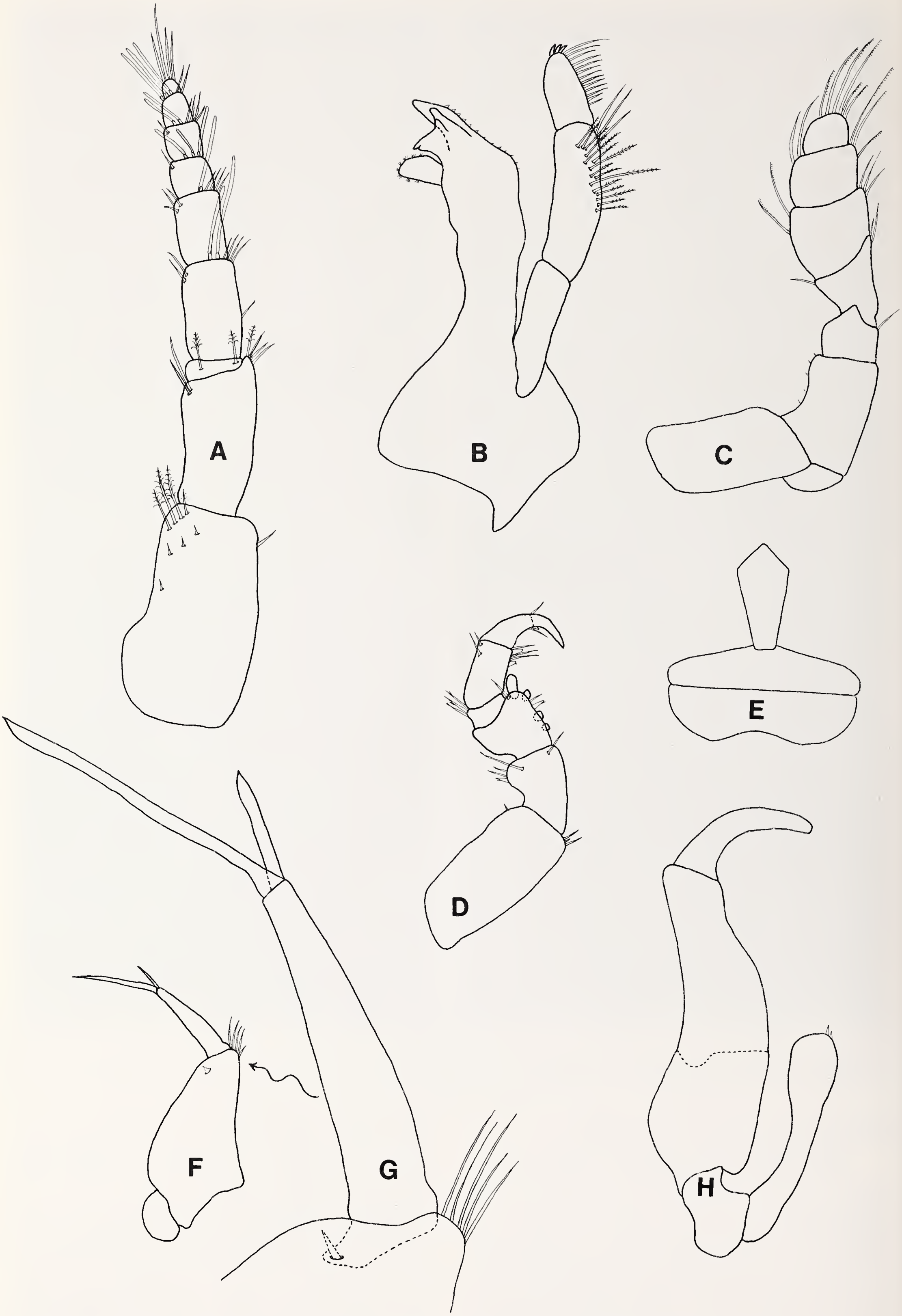
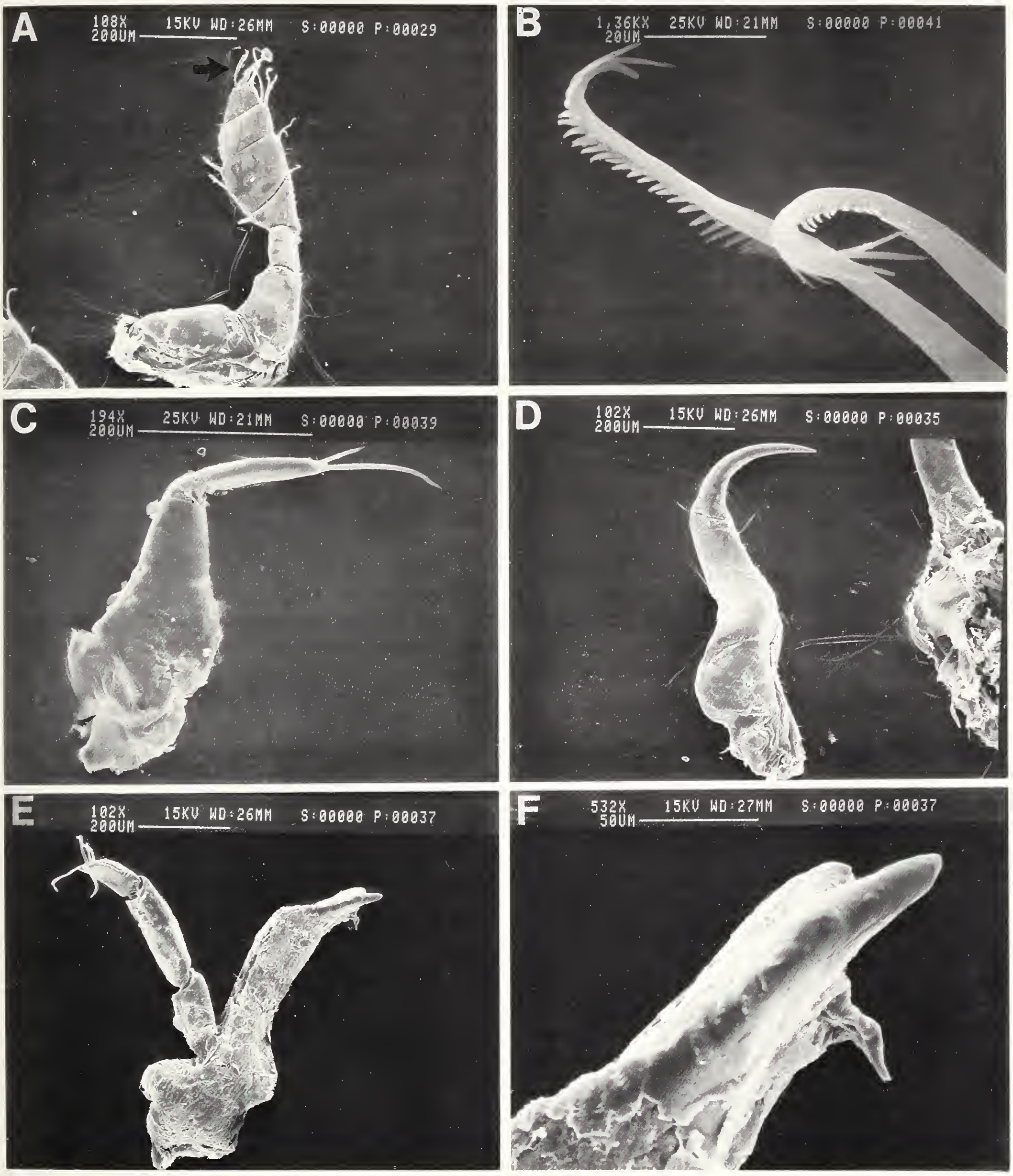


Figure 28. *Lanocira zeylanica,* USNM Acc. No. 93322: **A,** antennule; **B,** mandible; **C,** maxilliped; **D,** pereopod I; **E,** frontal lamina, clypeus, and labrum; **F,** maxilla; **G,** distal part of maxilla; and **H,** maxillule.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B
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20UM
C
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D
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200UM
E
102X 15KV WD:26MM S:00000 P:00037
200UM
F
532X 15KV WD:27MM S:00000 P:00037
50UM

**Figure 29.** Scanning electron micrographs of *Lanocira zeylanica,* USNM Acc. No. 93322: **A,** maxilliped; **B,** apical setae on maxilliped; **C,** maxilla; **D,** maxillule; **E,** mandible; and **F,** mandible apex.

(1982). Although Hansen's (1890) maxilla figure was 4-articulate, he considered the maxilla as being 3-articulate "with the first segment subdivided." Jones (1982) figured the maxilla of *L. anasicula* as 3-articulate with a partial suture on the first article, indicating that some fusion of articles may have occurred.

Loss or fusion of maxilliped palp articles does not occur in *Lanocira* as in *Argathona* and *Tachaea.* Jones (1982) discussed the number of articles in the maxillipeds of various *Lanocira* species but did not distinguish between the palp of the maxilliped (always 5-articulate in this genus) and the remainder of the maxilliped, i.e. the coxa and basis. Thus, Hansen (1890) and Moore (1902) were correct in describing maxilliped palps as 5-articulate but figuring maxillipeds with 7 articles in their species descriptions.

Some sexual variation is evident in the dorsal ornamentation of *Lanocira* species, as all other corallanid genera. Jones (1982) noted that females often lack the rostral process characteristic of male *L. gardineri, L. latifrons,* and *L. anasicula.* Thus, care should be taken when identifying females of those species.

Bruce (1980) noted that some authors have con-

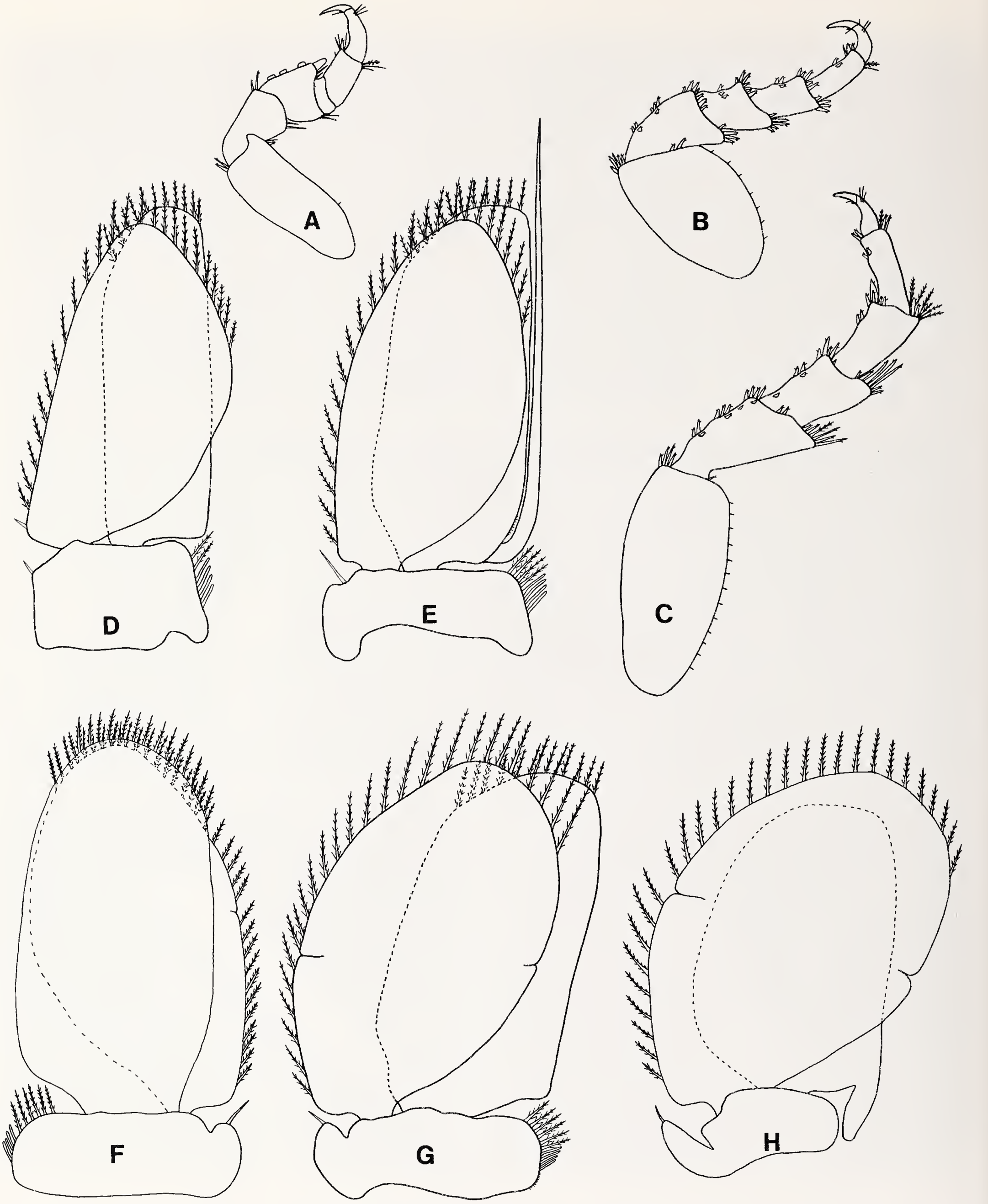


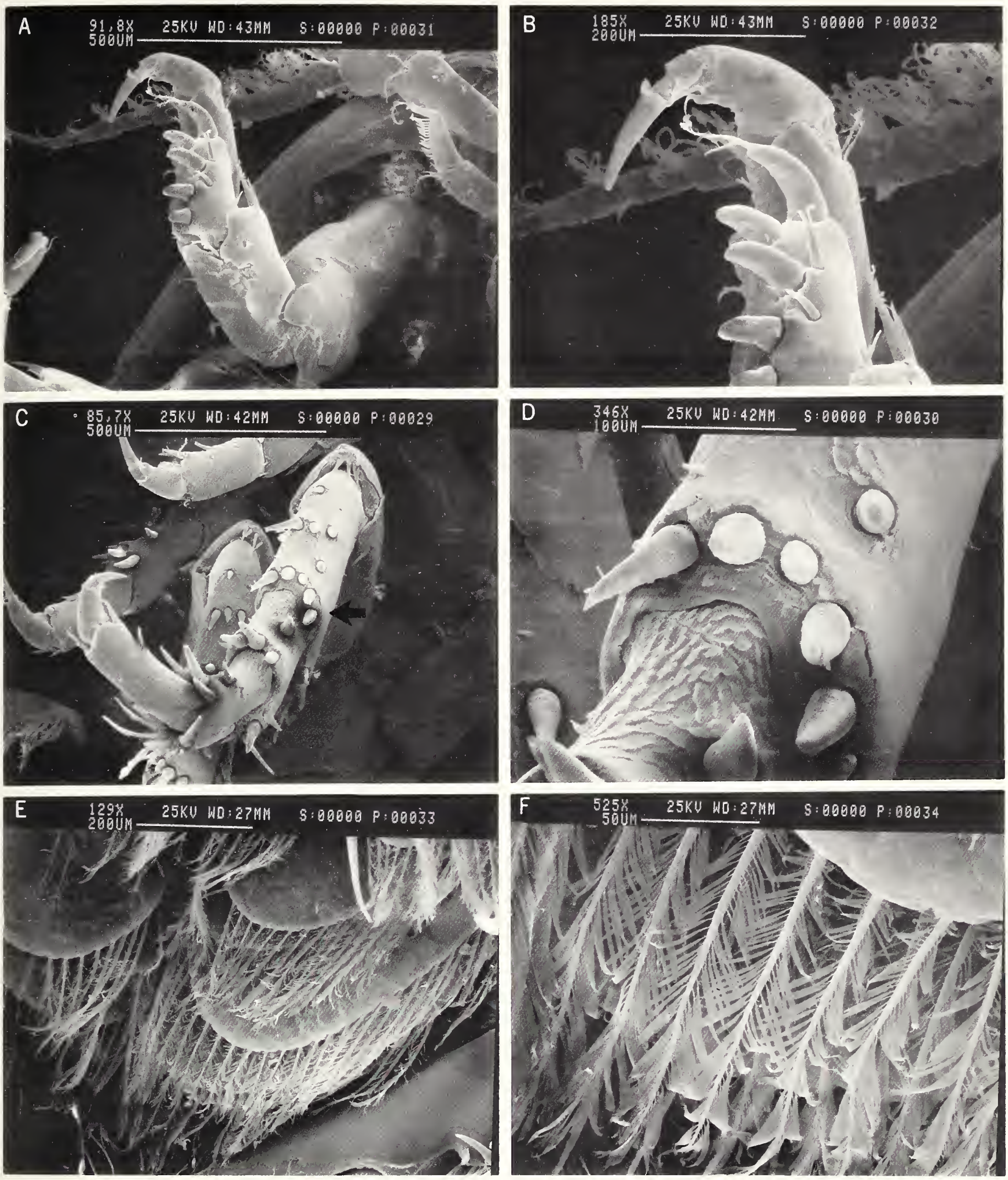
**Figure 30.** *Lanocira zeylanica*, USNM Acc. No. 93322: **A,** pereopod I; **B,** pereopod IV; **C,** pereopod VII; **D,** pleopod 1; **E,** pleopod 2; **F,** pleopod 3, **G,** pleopod 4; and **H,** pleopod 5.

sidered *Lanocira rotundicauda* a possible synonym of *L. gardineri* (Stebbing, 1905; Monod, 1933), but Pillai (1967) and Jones (1982) maintained them as distinct species. Barnard (1955) mentioned the possibility that *L. latifrons* is only the fully adult male of *L. gardineri* but maintained them as separate species (as did subsequent authors).

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The eight species of *Lanocira* are usually found in tropical/subtropical marine habitats. Five of the species are to be restricted to the Indo-West Pacific (*L. gardineri, L. rotundicauda, L. latifrons, L. glabra,* and *L. anasicula*). *Lanocira zeylanica* has the widest distribution in the genus, being known from throughout the Indo-West Pacific as well as from the Juan Fernandez Islands and Easter Island in the eastern South Pacific. *Lanocira rapax* and *L. kroyeri* are restricted to the Caribbean/Gulf of Mexico and Western Atlantic (Brazil) regions, respectively (Fig. 32).

*Lanocira* species have been found from the intertidal to depths of 120 m from substrates includ-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B
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C
85,7X 25KV WD:42MM S:00000 P:00029
500UM
D
346X 25KV WD:42MM S:00000 P:00030
100UM
E
129X 25KV WD:27MM S:00000 P:00033
200UM
F
525X 25KV WD:27MM S:00000 P:00034
50UM

**Figure 31.** Scanning electron micrographs of *Lanocira gardineri,* USNM 40956: **A,** pereopod I; **B,** propodus and dactyl of pereopod I; **C,** pereopod VI; **D,** spines on ischium of pereopod VI; **E,** apex of pleopods 4 and 5; and **F,** plumose marginal setae on pleopod 5.

ing live and dead corals, coral rubble, and sand. There is only one record (this study) of an unidentified *Lanocira* species collected as a "temporary parasite" of a fish (*Variola louti*), but there are a variety of "commensal" associations reported. *Lanocira gardineri* has been collected from sponges (Barnard, 1920; Bruce, 1980), from among the tubes of the worm *Sabellaria capensis* (Barnard, 1914), with ascidians (Stebbing, 1905), and from corals (Jones, 1982). *Lanocira zeylanica* has been collected from sponges (Monod, 1933) and from corals (Monod, 1933; Jones, 1982). *Lanocira latifrons* has been reported from "the umbrella of *Cassiopea andromeda* (Scyphozoa)" (this study). *Lanocira glabra* has been collected as an associate of algae and marine angiosperm rhizomes (Jones, 1982). *Lanocira anasicula* has been collected from *Montipora* corals (Jones, 1982).

Jones (1982) noted that many *Lanocira* species seem limited to hard substrates and may be restricted to cryptic habitats in sheltered waters, especially the crevices of live and dead corals. He also noted the absence of *Lanocira* from his plankton tows at Watamu, Kenya, and suggested that

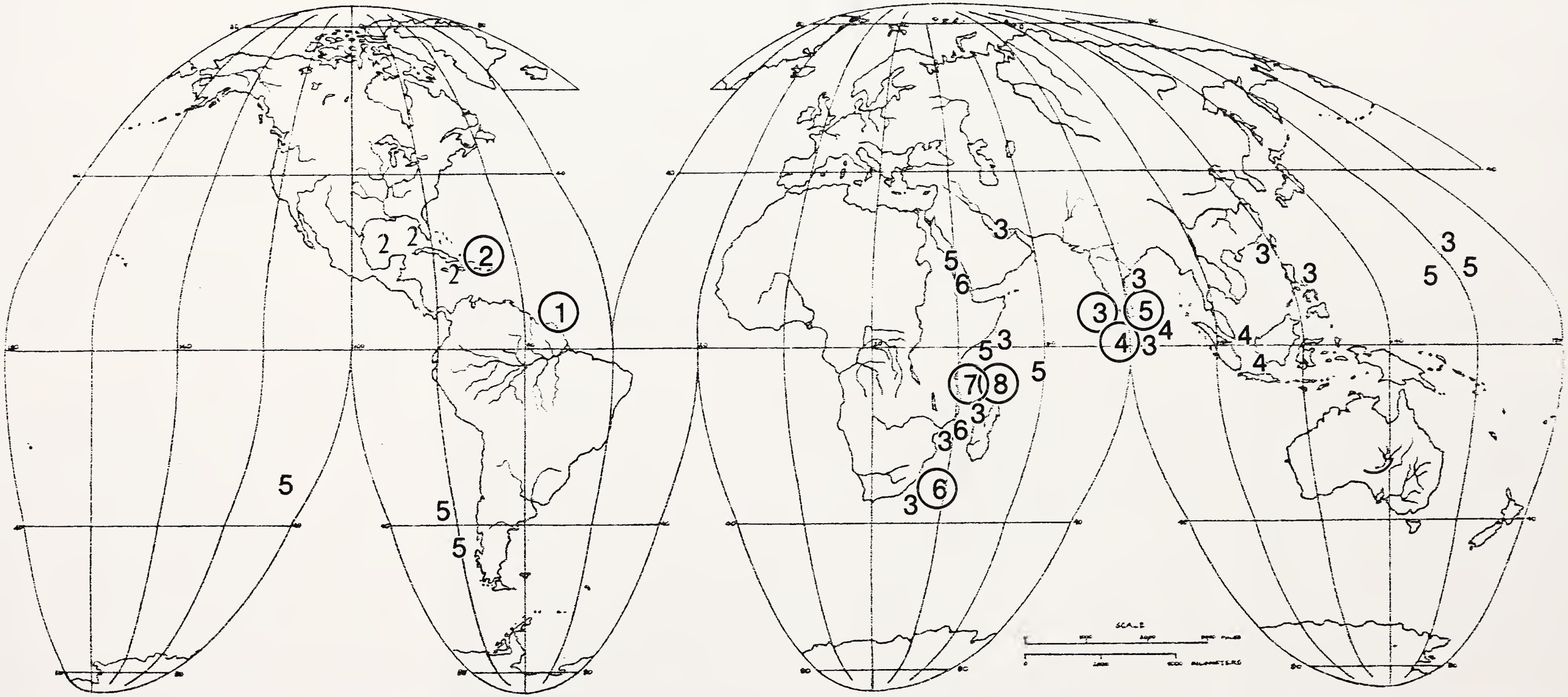

Figure 32. Distribution of *Lanocira* species; type localities are circled. Species numbers are: 1, *L. kroyeri;* 2, *L. rapax;* 3, *L. gardineri;* 4, *L. rotundicauda;* 5, *L. zeylanica;* 6, *L. latifrons;* 7, *L. glabra;* and 8, *L. anasicula.*

this absence, along with the morphology of the mandibles, implied omnivorous or herbivorous habits for *Lanocira*. The scarcity of fish "parasite" records gives some support to the contention of omnivorous habits for this genus.

Barnard (1920) noted that one specimen of *Lanocira capensis* (a synonym of *L. gardineri*) was parasitized by two cryptoniscan larvae, which he attributed to the genus *Clypeoniscus*.

## Genus *Tachaea*
## Schioedte and Meinert, 1879

*Tachaea* Schioedte and Meinert, 1879:284; Hansen, 1890:239; Weber, 1892:551; Stebbing, 1893: 315, 1904a:14, 1904b:703, 1907:39, 1908:107; Thielemann, 1910:18; Tattersall, 1921:419; Shen, 1936:17; Nierstrasz, 1917:102, 1931:172; Nierstrasz and De Marees van Swinderen, 1931:397; Bruce, 1982b:248; Bruce et al., 1982:464; Delaney and Brusca, 1985:729.

*Austroargathona* Riek, 1953:259, 1967:176; Bruce et al., 1982:464; Delaney and Brusca, 1985:729.

*Icochaea* Caldwell, 1879:38 (*lapsus calami*).

*Icochaes* Shen, 1936:17 (*lapsus calami*).

### MATERIAL EXAMINED

*Tachaea crassipes:* 1) no locality data, ZMUC, 1 spec., 4 mm (cephalon missing); 2) (as *Tachaea incerta,* type) ZMUC, 1 spec., 6.8 mm. *Tachaea lacustris:* 1) Java, ZMHUB No. 23023, "FF4d," Sunda Expedition, 3 fe., 8.9, 8.4, and 9.6 mm; 2) East Java, Lake Klakah, ZML No. 1288, Deutsch Limnologische Sunda Expedition, 1 ma., 10.1 mm, and 2 fe., 9.2 and 7.6 mm; 3) Java, Lake Klakah, USNM Acc. No. 100460, >20 spec. *Tachaea spongillicola:* India, Calcutta, BMNH syntypes, 1907-10-19-4, "In canals of *Spongilla carteri,*" 2 spec., 5.2 and 2.8 mm (cephalon and pleon missing). *Tachaea chinensis:* 1) Siam, Huai Nam Puat, USNM 142208, "HGD 114," 1 fe.; 2) Thailand, Ratchathani Province, Ubon Ubon, at morning market, USNM Acc. No. 309712, Smithsonian Institution, WBD-Mekong Program, Sta. T-1079, 15°13'30"N, 104°52'E, 1 spec.; 3) China, Hong Kong, USNM Acc. No. 312185, "Associated with oysters," 2 ma.; 4) China, Fukien, Haiteng, USNM Acc. No. 161481, 1 fe.; 5) Japan, Yokohama, ZMHUB, "From a pool with *Palaemon,*" 1 fe., 5.3 mm; 6) Japan, Tokyo, ZMHUB No. 6922, 1 fe., 6.6 mm; 7) China, Peking, ZMUC, 1 fe., 5.3 mm; 8) Malaya, Johore, Gunong Pulai, BMNH 1961-8-25-24-25, "On *Macrobrachium* sp.," 2 fe., 4.5 and 2.9 mm; 9) Japan, Honshu, Mie Prefecture, ZML, "Mouth of small stream near Toba, Kii Peninsula, brackish water," 2 fe. spec., 8.4 and 7.4 mm; 10) Japan, Tokyo, ZMHUB No. 6967, 1 fe., 6.3 mm. *Austroargathona caridophaga:* 1) Australia, Queensland, Conondale River, ZML No. 1715, paratypes, "Parasitic on *Macrobrachium,*" 2 fe., 9.0 and 6.6 mm; 2) Australia, Queensland, AM slides of holotype and allotype appendages. *Austroargathona picta:* 1) Australia, New South Wales, AM slides of holotype appendages. *Austroargathona* sp.: 1) Thailand, 3300 m N. of Udorn Thani, BMNH 1977-325-2, "Found on *Macrobrachium lanchesteri* in a rice field," 2 fe., 4.6 and 4.8 mm. *Tachaea* sp.: 1) New Guinea, Papua, Bootless Bay, Motupore Island, Port Moresby, USNM Acc. No. 320977, 1 fe.; 2) Undescribed species, NTM slides of ma. (N.L. Bruce.)

### DIAGNOSIS

Antennule peduncle 2-articulate; basal article expanded. Frontal lamina quadrangular, elongate, length = 2.0–3.0 times width; rounded anteriorly, narrowing posteriorly. Clypeus short, broad; labrum small. Mandible with small, monocuspid incisor; lacinia mobilis and molar process small or absent. Maxillule lateral lobe forming single large curved spine; medial lobe simple, with bluntly rounded apex. Maxilla short, 2- or 3-articulate, ending in rounded lobe. Maxilliped without endite; basis elongate, length = 1.5–2.0 times width; palp 3-, 4-, or 5-articulate, middle article not elongate. Anterior pereopods with carpi strongly produced on posteromedial margins; without serrate dactyli and propodi.

### ADDITIONAL DESCRIPTION

Eyes small, widely separated. Body occasionally with dorsal tubercles and setae (Figs. 1F, G). Antennule peduncle basal article expanded (Fig. 33F). Antenna peduncle articles 4 and 5 elongate (Fig. 33E). Frontal lamina, clypeus, and labrum visible anterior to mandibles; labrum may cover distal region of mandibular incisor. Clypeus sometimes encompassing lateral margins of labrum (Fig. 34A). Mandible molar process, when present, represented by small 3-spined lobe; lacinia mobilis represented by 1–3-spined lobe. Palp inserted near mandible base, 3-articulate, middle article longest, with simple marginal setae; distal article with plumose marginal setae and often with comblike cuticular structures (Figs. 33C, H, 35D, 36C–F). Maxillule lateral (outer) lobe forming single large curved spine, occasionally with 1 minute straight spine at base (in *T. picta*); medial (inner) lobe with single apical seta (Figs. 33I, 35G, 37C, F, 36A, B). Maxilla with 0–4 apical setae (Figs. 33D, J, 35E, 37C, E). Maxilliped palp distal articles with simple marginal setae (Figs. 33A, B, G, 35A–C, 37A, B, D). In gravid females, oostegites cover buccal field, and large epipods, with plumose marginal setae, arise from maxilliped bases (Fig. 35A). Pereopods I–III short, prehensile; with short bifid spines, simple spines and setae on posteromedial margins (Fig. 34B, C, 35F). Pereopods IV–VII longer, ambulatory, with spines and setae on posteromedial margins, and long propodi (Fig. 34D). Pleopod peduncles wider than long, with 4–5 cou-

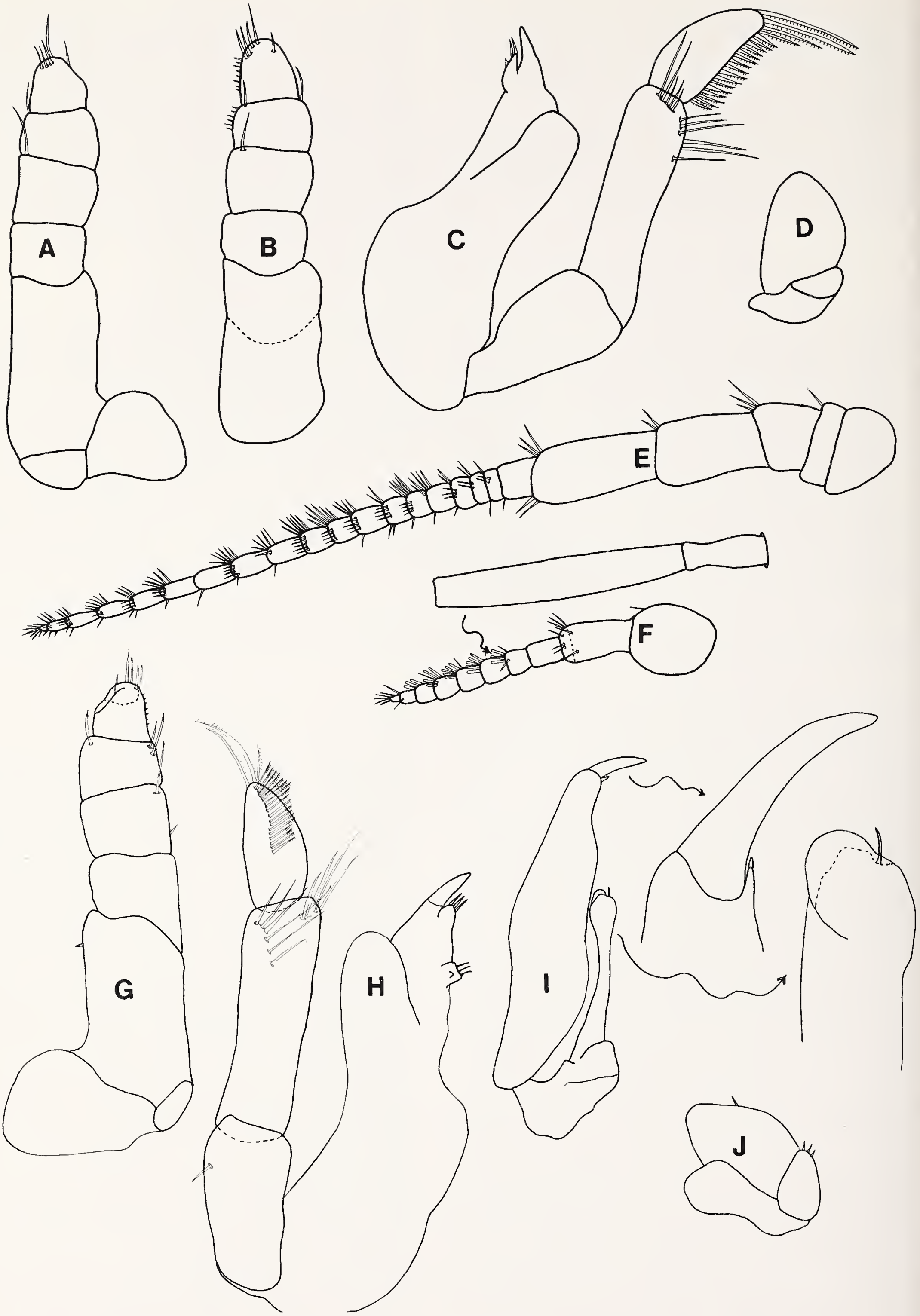

Figure 33. *Tachaea* sp., NTM, male one, A–F: **A,** left maxilliped; **B,** right maxilliped; **C,** left mandible; **D,** right maxilla; **E,** antenna; and **F,** antennule. Male two, G–J: **G,** left maxilliped; **H,** right mandible; **I,** left maxillule; and **J,** right maxilla.

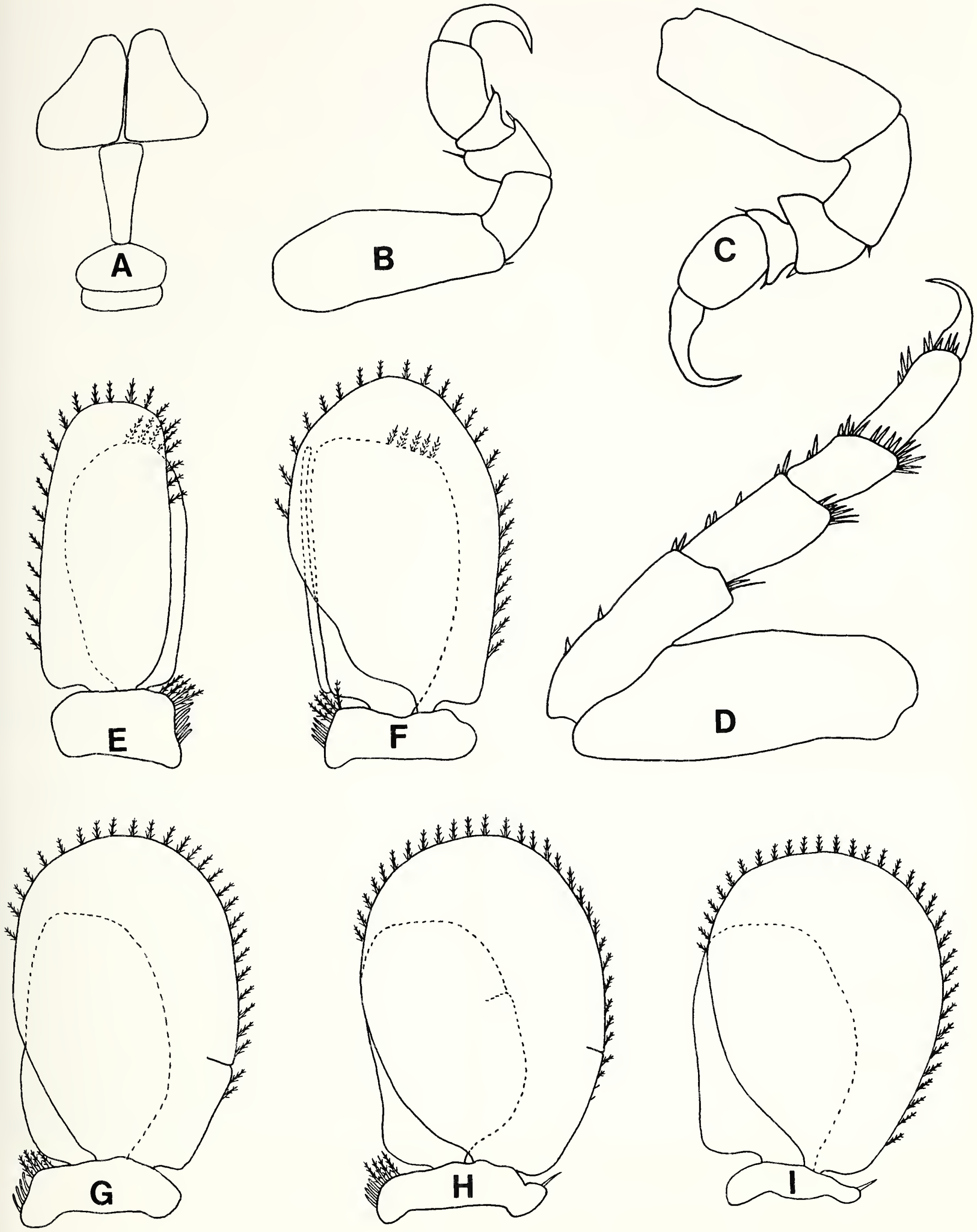

**Figure 34.** *Tachaea chinensis,* USNM 312185: **A,** antennule bases, frontal lamina, clypeus, and labrum. *Tachaea lacustris,* USNM Acc. No. 100460, B–I: **B,** pereopod I; C, pereopod III; **D,** pereopod VII; **E,** pleopod 1; **F,** pleopod 2; G, pleopod 3; **H,** pleopod 4; and **I,** pleopod 5.

pling spines and groups of proximal setae on medial margins, lateral margins often with simple spine (Figs. 34E–I). Exopods of pleopods broader, longer, and with more plumose marginal setae than endopods; endopod of pleopod 5 naked, endopods of 1–4 naked or with sparse setation. Male pleopod 2 with rodlike appendix masculina arising from proximal medial margin of endopod (Fig. 34F).

### TYPE SPECIES

*Tachaea crassipes* Schioedte and Meinert, 1879, by monotypy.

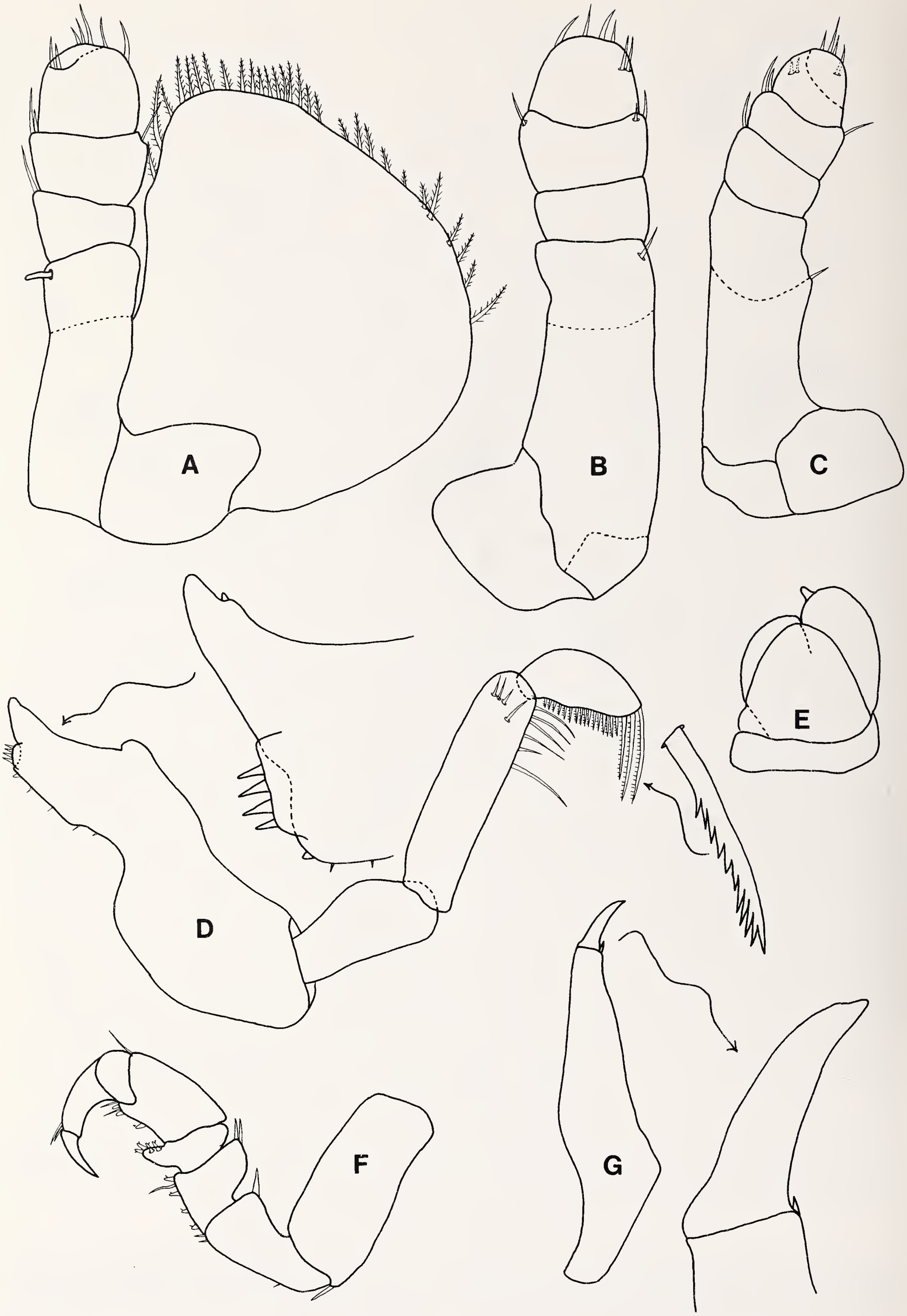

Figure 35. *Tachaea picta* (*ex Austroargathona*), AM holotype female, C–G: **A,** *T. caridophaga* (*ex Austroargathona*), holotype female, left maxilliped; **B,** *T. caridophaga*, allotype male, right maxilliped; **C,** right maxilliped; **D,** left mandible; **E,** left maxilla; **F,** pereopod I; and **G,** right maxillule.

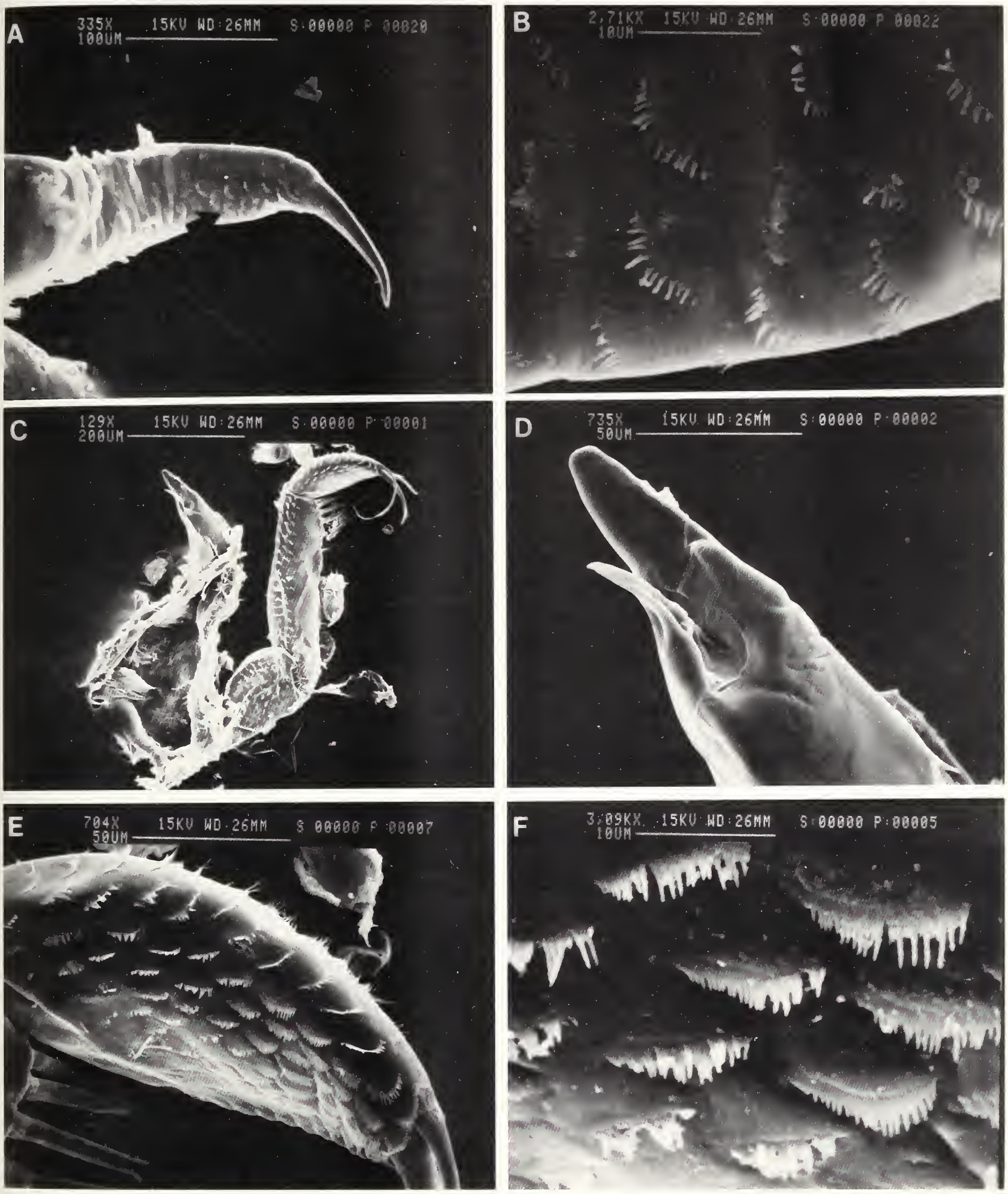
A
335X 15KV WD 26MM S 00000 P 00020
100UM
B
2.71KX 15KV WD 26MM S 00000 P 00022
10UM
C
129X 15KV WD 26MM S 00000 P 00001
200UM
D
735X 15KV WD 26MM S 00000 P 00002
50UM
E
704X 15KV WD 26MM S 00000 P 00007
50UM
F
3.09KX 15KV WD 26MM S 00000 P 00005
10UM

**Figure 36.** Scanning electron micrographs of *Tachaea lacustris,* USNM Acc. No. 100469: **A,** maxillule, lateral lobe; **B,** detail of maxillule (in A); **C,** mandible; **D,** mandible apex; **E,** distal article of mandibular palp; and **F,** comblike cuticular structures on distal article of mandibular palp.

## DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

1) *Tachaea crassipes* Schioedte and Meinert, 1879: 285, table IV, figures 2–7; Hansen, 1890:398; Weber, 1892:552; Stebbing, 1893:315, 1907: 41; Thielemann, 1910:21; Nierstrasz, 1917: 102, 1931:172; Tattersall, 1921:419; Nierstrasz and De Marees van Swinderen, 1931: 399; Shen, 1936:17.

*Tachaea incerta* Hansen, 1890:400, table IX, figures 2a, b; Weber, 1892:552; Stebbing, 1893: 315, 1907:41; Thielemann, 1910:21; Nierstrasz, 1917:102, 1931:172; Nierstrasz and De Marees van Swinderen, 1931:398.

*Ichochaes crassipes* Shen, 1936:17 (*lapsus calami*).

**DISTRIBUTION.** Singapore.

2) *Tachaea lacustris* Weber, 1892:551; Stebbing,

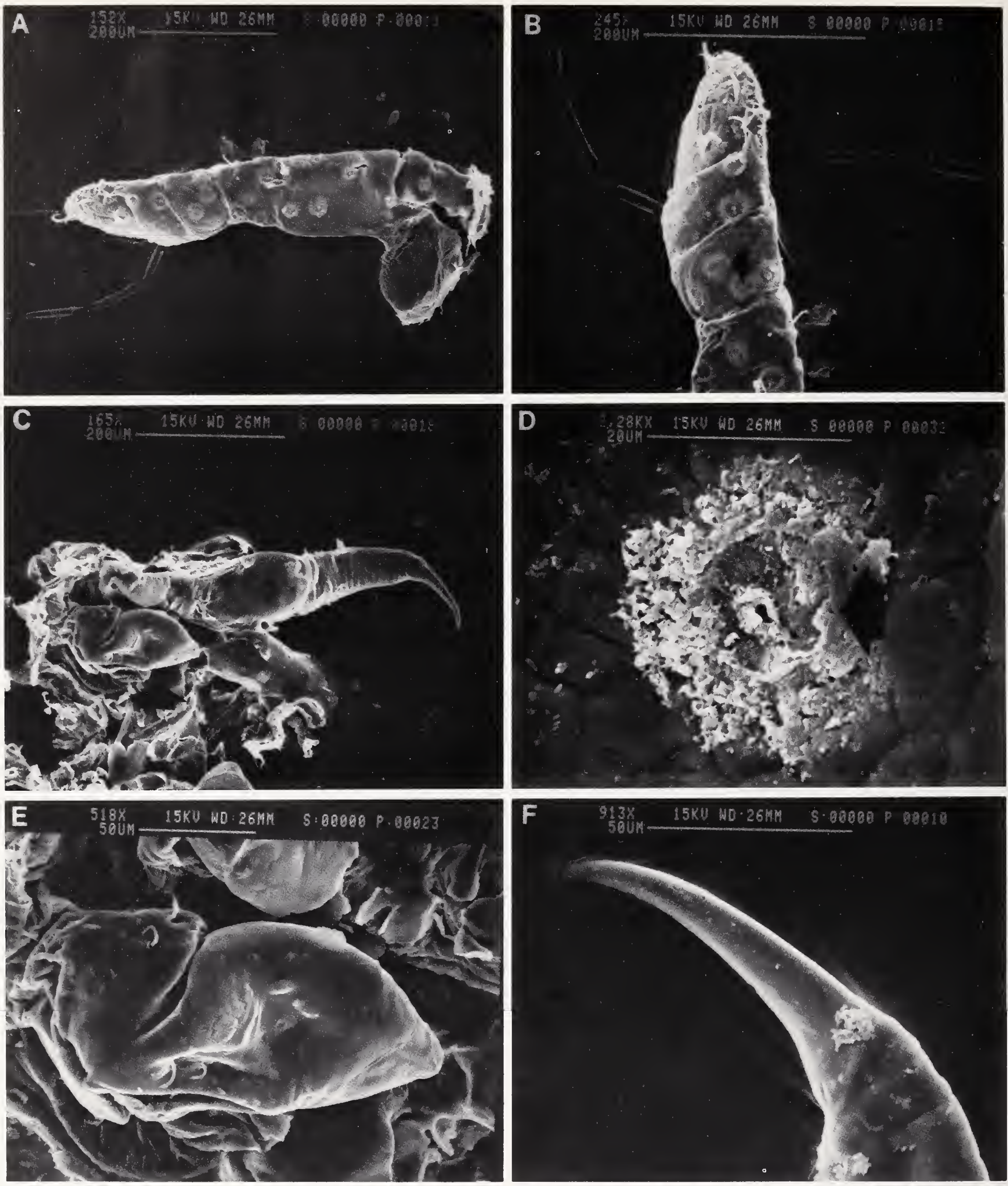

**Figure 37.** Scanning electron micrographs of *Tachaea lacustris*, USNM Acc. No. 100469: **A,** maxilliped; **B,** maxilliped palp; **C,** maxilla and maxillule; **D,** surface detail of maxilliped (arrow in B); **E,** maxilla; and **F,** maxillule apex.

1908:107; Thielemann, 1910:21; Nierstrasz, 1917:102, 1931:172; Tattersall, 1921:420; Nierstrasz and De Marees van Swinderen, 1931:397; Shen, 1936:17.

**DISTRIBUTION.** Sumatra and Java.

3) *Tachaea spongillicola* Stebbing, 1907:40, plate 6, 1908:107; Thielemann, 1910:21; Nierstrasz, 1917:102, 1931:172; Tattersall, 1921:419; Nierstrasz and De Marees van Swinderen, 1931:398; Shen, 1936:17.

**DISTRIBUTION.** India.

4) *Tachaea chinensis* Thielemann, 1910:19, figures 12–20; Nierstrasz, 1917:102, 1931:172; Tattersall, 1921:420; Nierstrasz and De Marees van Swinderen, 1931:399; Shen, 1936:17.

**DISTRIBUTION.** China, Japan, Thailand, and Malaya.

5) *Tachaea caridophaga* (Riek, 1953):259, figures 1–7.
*Austroargathona caridophaga* Riek, 1953:259.

**DISTRIBUTION.** Queensland, Australia.

6) *Tachaea picta* (Riek, 1967):176, figures 1–6. *Austroargathona picta* Riek, 1967:176.

**DISTRIBUTION.** Queensland and New South Wales, Australia.

## REMARKS

The genus *Tachaea* was established in 1879 by Schioedte and Meinert for their *Tachaea crassipes.*

The genus *Austroargathona* was erected by Riek in 1953 for his species *Austroargathona caridophaga* and was placed by him in the Corallanidae. A second species, *Austroargathona picta,* was added by Riek in 1967.

The validity of the genus *Austroargathona* has been suspect for some time, as was noted by Bruce et al. (1982). The 2 existing species of *Austroargathona* have morphological features typical of *Tachaea* species, including features of the antennules, antennae, mouthparts, and pereopods. Examination of type and non-type specimens, and comparison of morphological characters, has indicated to me that *Austroargathona* should be synonymized with the *Tachaea,* the latter having priority.

Although Riek (1953) did not mention the obviously similar *Tachaea* when comparing his new genus *Austroargathona* to other corallanid genera, the absence of molar process and lacinia on the mandible, the 3-articulate maxilliped palp, and the nonexpanded propodi of pereopods I–III were the only characters indicated that might distinguish *Austroargathona* from *Tachaea.*

The presence or absence of a molar process and lacinia mobilis on the mandible varies among species of *Tachaea.* Absence of a mandibular molar process has been noted in certain species of *Excorallana* (Richardson, 1905; Delaney, 1982, 1984) and *Alcirona* (Richardson, 1905; Hale, 1925; Menzies and Glynn, 1968; Menzies and Kruczynski, 1983).

From examination of *Tachaea* and *Austroargathona* specimens I have found that the number and extent of maxilliped article fusion/loss may vary within species (as in *T. chinensis,* see Thielemann, 1910, and Shen, 1936) as well as among species. The second corallanid species described by Riek (1967), *Austroargathona picta,* possesses a 4-articulate maxilliped palp. Apparent fusion or loss of maxilliped articles is known in various *Tachaea* species such as *Tachaea crassipes* Schioedte and Meinert, 1879 (in Hansen, 1890), *T. spongillicola* Stebbing, 1907, and *T. chinensis* Thielemann, 1910. Tattersall (1921) noted that various degrees of maxilliped fusion have been described in *Tachaea:* fusion of 2nd and 3rd articles (by Hansen, 1890); 6th and 7th articles (by Stebbing, 1907); 2nd–3rd and 6th–7th articles (by Thielemann, 1910); and no fusion or loss of articles at all (Shen, 1936). Tattersall (1921) also noted that fusion may be incomplete, as evidenced by partial suture lines on the maxillipeds of *T. chinensis* Thielemann. Loss or fusion of maxilliped palp articles is also recorded in certain species of *Argathona* (Stebbing, 1905, 1911; Hale, 1925; Monod, 1933, 1975; Barnard, 1936; Pillai, 1967; Bruce, 1982b). Loss and/or fusion of maxilliped palp articles also commonly occurs in many other families of isopods.

Lastly, the carpi of pereopods I–III are produced in both *Tachaea* and *Austroargathona.*

The name *Icochaea crassipes* was published in the *Zoological Record* for 1879 (Caldwell, 1879: 38) and attributed to Schioedte and Meinert, but does not appear in either of their publications that year. Shen (1936) misspelled the name as *Icochaes crassipes* but indicated that it and *Tachaea incerta* should be regarded as junior synonyms of *T. crassipes. Icochaea* and *Icochaes* should be regarded as incorrect subsequent spellings (*lapsus calami*) of the correct genus name *Tachaea.*

Sexual dimorphism exists in the dorsal ornamentation of some *Tachaea* species, as in all other genera of the Corallanidae and Tridentellidae. In *Tachaea lacustris* males have a pair of anterior cephalic tubercles as well as large tubercles on the posterior pereonites; these structures are lacking in females (see Nierstrasz and De Marees van Swinderen, 1931:398).

Stebbing (1907) noted that in *Tachaea spongillicola* the pleotelson is broadly rounded in females but is apically truncate in males. Based on this information he synonymized *T. incerta* Hansen with *T. crassipes* Schioedte and Meinert. Stebbing distinguished *T. spongillicola* from *T. crassipes* by the apical article of the maxillipeds as well as the decreased spination of the pereopods and the shorter pleon (relative to pereon length) in the former species.

Nierstrasz and De Marees van Swinderen (1931) redescribed *Tachaea lacustris* Weber and noted much variation in the number of antenna flagellar articles, pleotelson spination, and pleotelson shape, which they found to vary from rounded to "somewhat pointed."

*Tachaea leopoldi* Nierstrasz, 1930, was removed to the genus *Corallana* by Bruce (1982b).

*Tachaea picta* Riek, 1967, is very similar to *T. caridophaga* Riek, 1953, and may prove to be a junior synonym. However, until more specimens can be examined they must remain separate species.

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The six described species of *Tachaea* show a range in habitat and distribution that is more restricted than that of any other genus in the family Corallanidae, being confined mainly to tropical/subtropical freshwater habitats in the Indo-Pacific region (Fig. 38). One species, *T. crassipes,* has been reported as marine (from coral reefs, Singapore), while the other five species, from freshwater ponds, lakes, and rivers, have been reported as "ectoparasites" of fish (*Culter brevicauda,* "Cyprinoiden" fish, and "catfish") and various shrimp species (*Ca-*

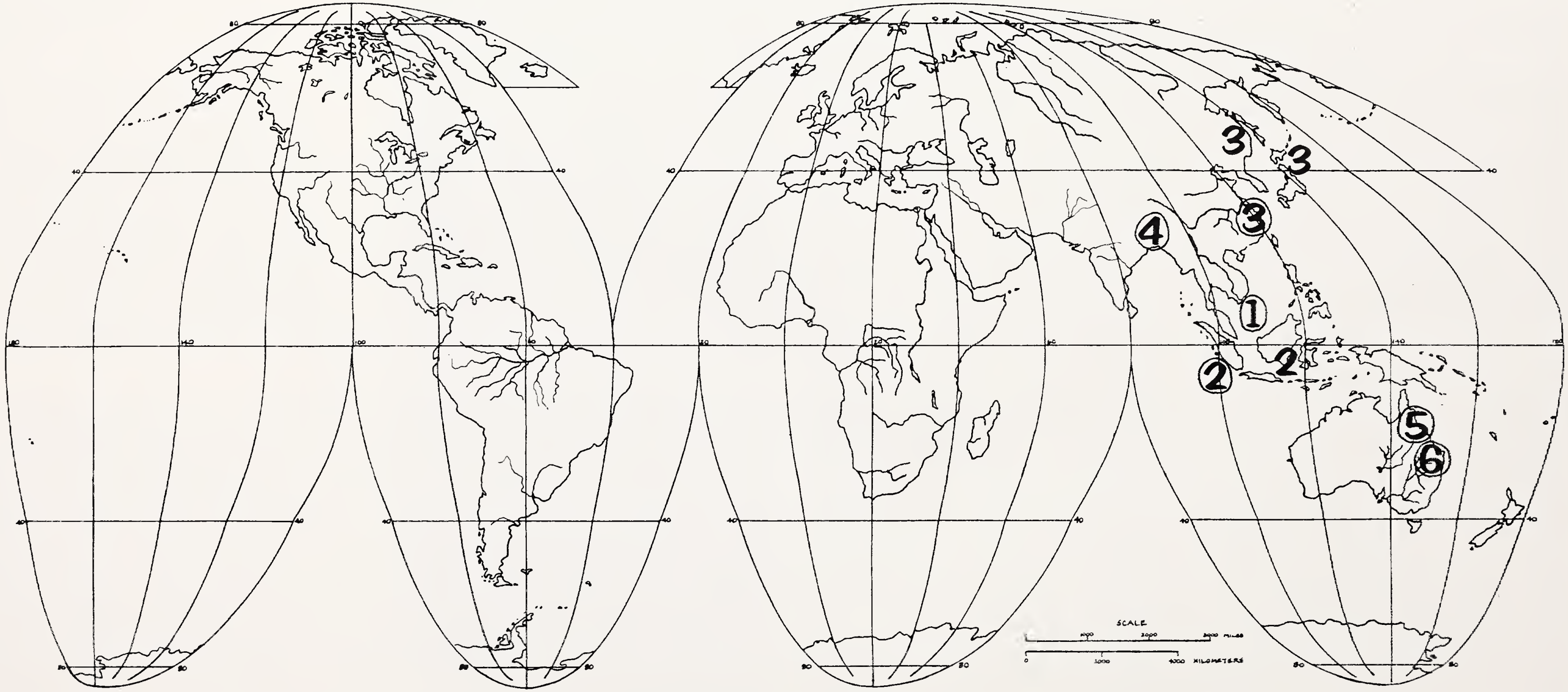

Figure 38. Distribution of *Tachaea* species; type localities are circled. Species numbers are: **1**, *T. crassipes;* **2**, *T. lacustris;* **3**, *T. chinensis;* **4**, *T. spongillicola;* **5**, *T. caridophaga;* and **6**, *T. picta.*

*ridina nilotica gracilipes, Caridina denticulata, Palaemonetes sinensis, Leander paucidens, Macrobrachium australiense cristatum, Macrobrachium lanchesteri, Macrobrachium* sp., *Palaemon* sp., and *Paratya* sp.). Other *Tachaea* species have been collected as "commensals" of freshwater sponges (*Spongilla carteri* or *Spongilla lacustris*) and as associates of oysters, hydroids, and the burrows of larval *Povilla corporaali.*

## CLADISTIC ANALYSIS

## MATERIALS AND METHODS

### General Methods

Cladistic relations between the six currently recognized genera of the isopod family Corallanidae and the outgroup families Tridentellidae and Cirolanidae were determined by analyzing sets of morphological character states using the PAUP computer program of Dr. David Swofford (Version 2.4) and the PHYLIP package of Dr. Joseph Felsenstein (Version 2.7), as adapted and compiled for IBM personal computers by Dr. George D.F. Wilson. The philosophical methods used in this study were largely summarized in three recent texts (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981).

Nomenclature and terminology were taken from current literature on the families Corallanidae, Tridentellidae, and Cirolanidae (see Delaney and Brusca, 1985). Characters used in the analysis were mostly traditional characters used to define corallanid genera (see Bruce et al., 1982), such as morphology of the mouthparts and pereopods, as well as additional characters of antennules, eyes, pleotelson, and frontal laminae. Character states were determined by examining type-species and type-specimens whenever possible, but all materials examined were used to diagnose the characters for each corallanid genus. Fifty trees resulting from PAUP and PHYLIP were compared for topology and tree length. Homoplasy statistics, if provided by the program, were also compared. Each tree is referred to by the program that generated it and by number. For example, the PAUP tree in Figure 39 is referred to as PAUP 1 in the text and Table 4, and the DOLLOP tree 17 is called DOLLOP 17 in Table 4. The object of this analysis was to find the tree that was the most parsimonious in terms of minimum tree length (= number of character state changes) and minimum homoplasy (= number of convergences and reversals required for the construction of the particular tree), as well as being the tree most corroborated by topologies produced from the other cladistic algorithms.

### Character Coding

The numerical coding of characters is an extremely important part of cladistic analysis. The coding procedure requires the systematist to convert his knowledge of the variation within and between taxa into numerical format. This almost always involves some subjectivity on the part of the systematist, whether acknowledged or not.

Some features of corallanid genera were easier to code than others, and these have straightforward character state descriptions. However, some characters required more ambiguous character state descriptions. For example, many *Alcirona* species possess serrated dactyli on pereopod I, yet not all species in that genus do. Therefore, the character state description (see Appendix II) for that character reads "without serrate dactyli" for genera in which the condition has never been observed, and "with serrate dactyli in some species" for genera where this state has been observed, though not necessarily in all species. I consider this a valid way of including characters that are variable within a genus and yet contain useful phylogenetic information.

### Out-groups and Character State Ordering

The polarity of transformation series of character states were initially established by out-group analysis, using two related flabelliferan families, the Cirolanidae and Tridentellidae (for methods see Eldredge and Cracraft, 1980; Watrous and Wheeler, 1981; and Maddison et al., 1984). The Cirolanidae includes approximately 35 genera, while the Tridentellidae is monogeneric (*Tridentella*). Analyses with PAUP were done using these polarized ("ordered") multistate characters and with unpolarized characters (see Appendices II and III for character list and data matrices). These multistate characters were then recoded into binary character state data using the FACTOR program in PHYLIP. This binary state character set was analyzed with the PHYLIP programs WAGNER, DOLLOP, PENNY, MIX (parsimony optimization), and CLIQUE (compatibility optimization) for comparison to PAUP-generated trees. The evolutionary assumptions in PAUP and PHYLIP algorithms are compared in Table 2.

### Methods Used with the PAUP Program

PAUP trees were produced from an 8-taxon, 21-character multistate data matrix. Both "directed" and "undirected" analyses were performed. In the "directed" analysis, the families Cirolanidae and Tridentellidae were the designated out-groups used to polarize character states. Each of the two out-groups were used in turn to root the tree. However, trees of similar topology, identical length, and consistency index were produced each time. Subsequently, "undirected" analyses were performed in which the "unordered characters" option was used.

The "Alltrees" option was used; this is the exhaustive search option evaluating all possible tree topologies, computing the length of each and finding the absolute shortest, most parsimonious tree.

### Methods Used with the PHYLIP Programs

The set of multistate characters used in the PAUP analysis was recoded into binary characters using

Table 2. Comparison of different cladistic programs used in this study.

| Program | Function |
|---|---|
| PAUP | Unrestricted parsimony method = reversals and parallelism/convergences equally probable in explaining synapomorphy distributions. |
| PHYLIP | A package of cladistic programs (as follows). |
| WAGNER | Unrestricted parsimony = reversals and convergences equally probable. |
| DOLLOP | Restricted parsimony = allows one forward character change plus as many reversals as necessary. |
| PENNY | Unrestricted parsimony = WAGNER parsimony with "branch and bound" tree search method. |
| CLIQUE | Character compatibility method = seeks groups of mutually compatible characters to explain maximum number of synapomorphies. |
| MIX | Restricted Camin-Sokal parsimony = allows forward character changes but not reversals. |
| ITERMIX | Generates data sets with the order of taxonomic units randomized. |
| FACTOR | Recodes multistate characters using additive binary coding. |

the FACTOR program in PHYLIP as follows. Each multistate character to be factored was described by a list of pairs of character states that are adjacent to one another on a hypothesized character state tree. An ancestral state was not designated for any of the recoded characters. However, FACTOR requires that character states be coded as transforming from one particular state to another—a hypothesis of character state evolution (a character state tree). The result was an 8-OTU, 32-character data set (Appendix III); the recoding of multistate characters into binary ones produced an additional 11 characters.

Unlike PAUP, some programs in PHYLIP are known to be sensitive to order of OTUs in the data set. Therefore, 10 versions of the binary data set, with the order of the OTUs randomized, were constructed using the ITERMIX program in PHYLIP. These randomized versions were each analyzed with WAGNER, DOLLOP, and MIX (Camin-Sokal parsimony option) but not with PENNY or CLIQUE, as according to Felsenstein (1984) these latter two are not sensitive to the input order of OTUs, making multiple runs of the data set unnecessary.

## RESULTS AND DISCUSSION

Table 3 summarizes the results from various cladistic programs used in terms of: number and type of characters used; number of trees produced per iteration; length of trees and associated statistics such as consistency index (C.I.) and F-values, if such were given by the program. The program results are compared below.

### PAUP and PHYLIP Parsimony Analyses

The tree produced by the unordered PAUP analysis (Fig. 39) was generated from a completely "unordered" matrix of character states—no direction of evolutionary transformation was presumed for any character or used to impose a particular order on the cladogram. This topology was subsequently rooted using the designated out-groups to produce the directed tree PAUP 1. Meacham (1984) presents arguments supporting initial use of "undirected characters" in cladistic analyses and the subsequent directing of the undirected tree. PAUP 1 (Fig. 39) was the shorter tree (length = 32), had a higher consistency index (C.I. = 1.0), and was less ambig-

Table 3. Cladistic analysis of Corallanidae: results from different programs.

| Program | Characters | Trees produced | Comments |
|---|---|---|---|
| PAUP | 21, multistate | 1 tree, length = 32, C.I. = 1.0 | "unordered," unrestricted parsimony |
| PAUP | 21, multistate | 5 trees, length = 39, C.I. = 0.821, F-values = 28.0–48.0 | "ordered," unrestricted parsimony |
| WAGNER* | 32, binary | 5 trees, length = 39 (10 iterations: data input order randomized) | unrestricted parsimony |
| DOLLOP* | 32, binary | 1 tree, length = 41 (10 iterations: data input order randomized) | restricted parsimony |
| PENNY* | 32, binary | 5 trees, length = 39 | unrestricted parsimony (branch and bound method) |
| CLIQUE* | 32, binary | 9 cliques/trees, 25 characters, length = 25 | character compatibility analysis |
| MIX* | 32, binary | 4 trees, length = 40 (10 iterations: data input order randomized) | restricted Camin-Sokal parsimony |

* Programs from the PHYLIP package.

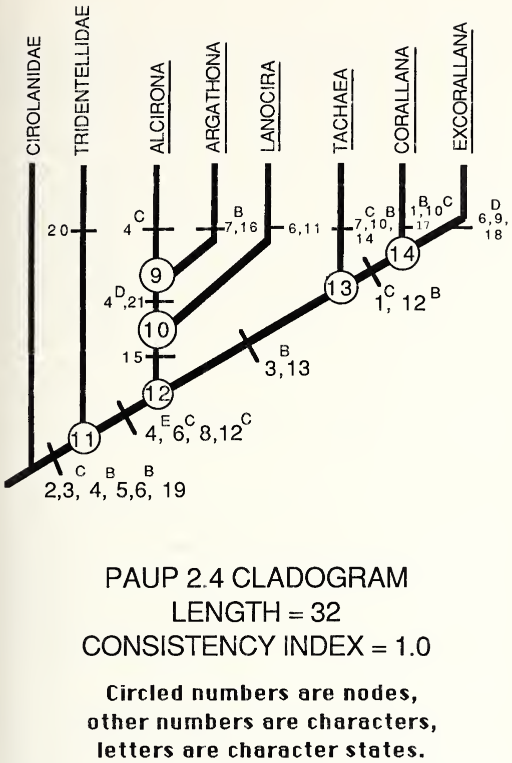

**Figure 39.** PAUP tree 1, produced from unordered characters.

uous (one tree) than those PAUP trees resulting from ordered characters (length = 39, C.I. = 0.821, five trees), as well as the trees produced from the WAGNER, DOLLOP, PENNY, and MIX (Camin-Sokal option) algorithms in PHYLIP (Table 3). The PAUP 1 tree (Fig. 39) was not only shorter than all other trees produced from programs using the entire data matrix (i.e. excluding compatibility analysis—CLIQUE), it was also corroborated by trees and cliques from more algorithms than any other PAUP or PHYLIP topology (Table 4).

## CLIQUE (PHYLIP) Analysis of Character Compatibility

Seventy-eight percent (25/32) of all characters were included in at least one of the nine cliques produced by this analysis; 66% (21/32) of all characters in the original data set were common to all nine cliques, indicating some character congruence. Eighty-four percent (21/25) of characters found in cliques were common to all cliques. Binary characters 5 and 15 were excluded from all of the nine cliques. These are binary characters recoded from multistate characters, meaning that some character states of certain multistate characters were excluded from cliques while others were not.

Thirty-four percent of the characters in the data set were "new" ones resulting from binary recoding. None of the cliques included all the binary characters produced from all the multistate characters.

As noted by Felsenstein in the documentation to PHYLIP 2.7, cliques of characters found by CLIQUE are cliques of two-state characters. If these are "binary-factors" recoded from multistate characters (by additive binary coding), some of the two-state characters from one multistate character may be involved in a clique and others *not involved.* For example, the two multistate characters of maxilla and maxillule morphology, when recoded into binary, made eight binary characters; in only one clique do all eight appear. As previously noted, binary characters 5 and 15 (each previously a part of a multistate character) do not appear at all. It is quite possible that this skews the meaning of "compatibility" for characters recoded in such a fashion and may be responsible for some of the differences in the nine cliques produced in this analysis. The creation of binary characters from multistate characters may weight those multistate characters in the analysis, and this implies that fundamental differences may exist between multistate and recoded, non-multistate trees.

**Table 4.** Corroborating trees and cliques for variant PAUP topologies.*

| PAUP topologies and statistics | Corroborating trees and cliques | Number of supporting trees/ programs |
|---|---|---|
| PAUP 1 (length = 32, C.I. = 1.0, no F-value) | PAUP 6; WAGNER 9, 10; PENNY 27; CLIQUE 35, MIX 43, 45, 46, 49 | 9/5 |
| PAUP 2 (length = 39, C.I. = 0.821, F-value = 48.0) | WAGNER 7; DOLLOP 17–26; PENNY 29 | 12/3 |
| PAUP 3 (length = 39, C.I. = 0.821, F-value = 40.0) | WAGNER 8, 15, 16; PENNY 28; CLIQUE 32, 33 | 6/3 |
| PAUP 4 (length = 39, C.I. = 0.821, F-value = 28.0) | WAGNER 11, 12, 14; PENNY 31; CLIQUE 40; MIX 50 | 6/4 |
| PAUP 5 (length = 39, C.I. = 0.821, F-value = 28.0) | WAGNER 13; PENNY 30 | 2/2 |

* Program name and number indicate individual trees.

## Choice of Final Cladogram

Comparison of the results produced by PAUP and PHYLIP shows the PAUP tree produced from unordered characters (and subsequently rooted with the designated out-groups), PAUP 1 (Fig. 39), is the most highly corroborated cladistic relationship for the genera of Corallanidae. PAUP 1 is supported by trees and cliques from more different programs than any other topology (Table 4). Other variant topologies are represented by the ordered PAUP trees (PAUP 2–5), which are also supported by trees or cliques from various PHYLIP programs, but not to the extent of PAUP 1, especially considering its length and consistency index. PAUP 1, constructed using the unrestricted parsimony criterion, minimized homoplasy and tree length and maximized the amount of information about cladistic relations in the Corallanidae, while avoiding unwarranted assumptions about evolutionary rates and the probabilities of different kinds of events (as in some PHYLIP programs which prefer reversals over convergences, etc.).

In addition to providing maximum parsimony and corroboration, PAUP: 1) allowed multistate character descriptions, which corresponded to the biological reality of corallanid genera (i.e. the evolutionary differentiation of some structures has produced more than two character states); 2) was an unrestricted parsimony method, i.e. it did not force assumptions about whether character reversals or independent acquisitions (convergence/parallelism) were more probable; 3) allowed the use of "unordered" characters, removing at least some bias towards polarization of character states; 4) provided character state data and statistics useful in choosing between trees; and 5) produced the shortest tree (excluding CLIQUE, which did not utilize the entire data set), with the highest consistency index. Accordingly I offer PAUP 1 (Fig. 39), rooted with Tridentellidae as the sister-group, as the best estimate of cladistic relations among the genera of Corallanidae.

## General Character Trends in the Final Cladogram

In the final (rooted) PAUP cladogram (PAUP 1), most of the now-polarized character changes involve reduction and simplification of cephalic appendages, tending to follow Brown's (1965) "Rule of Evolutionary Reduction."

Simplification and reduction of appendages in the Corallanidae from cirolanid/tridentellid morphologies involve the following character state transitions. The antennule peduncle is reduced from 3- to 2-articulate, and the basal article is expanded. The broad, short-incisored cirolanid mandible is transformed to a more slender-trunked, long-incisored mandible (such as in *Excorallana*) with reduction in size and spination of the molar process and with reduction or loss of the lacinia mobilis. The apex of the lateral lobe of the maxillule undergoes reduction of spine number, but an increase in size of one to two unique spines; the medial lobe likewise undergoes simplification of the apex, with loss of robust circumplumose spines and greatly reduced setation. The maxilla loses an entire lobe (becoming uniramous) and has the apex of the remaining lobe variously modified, but is always simplified, with reduced setation. The maxillipeds lose the endite, undergo fusion or loss of palp articles several times, and gain an elongate basis or elongate middle article in the palp. The pereopods, eyes, and pleotelson show unique modifications in various corallanid genera.

## Specific Character State Changes in the Cladogram

The following is a step-by-step discussion of the cladogram (Fig. 39) chosen as the one most representative of true cladistic relations between the corallanid genera and two out-groups, the Cirolanidae and Tridentellidae, for the reasons discussed above. Numbers in parentheses correspond to character apomorphies in the cladogram, and letters are character states.

The Tridentellidae and the Corallanidae are distinguished from the out-group Cirolanidae by the following characters: (2) mandible with molar process reduced in spination or size, or absent (3C) mandible with lacinia mobilis absent; (4B) maxillule lateral lobe apex with 3–5 stout hooked spines and several smaller subapical spines; (5) maxillule medial lobe with simple apex, without 3–4 robust, circumplumose spines; (6B) maxilla uniramous (i.e. without medial and lateral lobes); and (19) frontal lamina always flat, not projecting.

Synapomorphies uniting the corallanid genera and distinguishing them from the tridentellids are as follows: (4E) maxillule with single large falcate spine; (6C) maxilla forming a short, rounded lobe; (8) maxilliped without endite; and (12C) antennule peduncle 2-articulate.

The synapomorphy separating "Lineage A"—*Lanocira*, *Alcirona*, and *Argathona*—from cirolanids, tridentellids, and the other corallanid genera ("Lineage B"—*Tachaea*, *Corallana*, and *Excorallana*) is (15) first pereopod dactylus with serrations or dentate processes on margin.

Within Lineage A, *Lanocira* is differentiated from *Argathona* and *Alcirona* by these autapomorphies: (6) maxilla 3–4-articulate, apical article sublinear/elongate; and (11) mandible with row of dentate processes behind incisor.

The genera *Argathona* and *Alcirona* are distinguished from *Lanocira* by possession of (4D) maxillule lateral lobe apex with 1 large falcate spine and 1–3 smaller, hooklike, subapical spines (*Lanocira* having a single large falcate spine and no small accessory spines), and (21) medial lobe of maxillule distally expanded, with truncate apex.

*Argathona* is distinguished from *Alcirona* by the following synapomorphies: (7B) maxilliped palp 4–

5-articulate (versus always 5-articulate in *Alcirona*); and (16) eyes divided by unpigmented, transverse band in some species.

*Alcirona* is distinguished from its sister-group *Argathona* by (4C) maxillule medial lobe apex with 2 large falcate spines and 0–3 small accessory spines between the large ones.

Lineage B is separated from Lineage A by having (3B) a small lacinia mobilis on the mandible (apparently lost in the tridentellids and Lineage A, but regained here), and (13) basal article of antennule peduncle expanded.

Within Lineage B, *Tachaea* is distinguished from *Corallana* and *Excorallana* by: (7C) maxilliped palp 3–5-articulate; (10B) maxilliped basis elongate (length = 1.5–2.0 times width) (but not narrow as in *Corallana*); and (14) inner angle of pereopod I carpus produced.

*Corallana* and *Excorallana* are separated from *Tachaea* by the following synapomorphies: (1C) mandible with incisor elongate; (12B) antennule peduncle 2–3-articulate (versus 2-articulate in all other corallanid genera).

*Corallana* has the following apomorphies: (1B) mandibular incisor either short or long (several *Corallana* species show this condition, while most others have much shorter mandibular incisors; it is always long in *Excorallana*); (10C) maxilliped slender, basis narrow and very elongate (length = 2.0–4.0 times width); and (17) frontal lamina sometimes reduced or absent.

*Excorallana* is distinguished from *Corallana* by the following autapomorphies: (6D) maxilla with apex bi- or trilobed; (9) maxilliped palp with middle article elongate; and (18) many species in genus with lateral incisions in pleotelson.

## BIOGEOGRAPHY AND PHYLOGENY

### INTRODUCTION

As noted by McDowall (1978) and Brusca (1984), one can never know with certainty whether any given generalized biogeographic track is the product of a single vicariant event or numerous dispersal events. It is possible to narrow the search for pertinent vicariant events using knowledge of cladistic (sister-group) relationships and distribution patterns of endemic taxa. The existence of both vicariant and dispersal phenomena in the real world is certain, thus the task in this analysis was to decide which of these phenomena was most likely responsible for the biogeographic patterns seen in the genera of the Corallanidae today. Simpson (1980) summed up this philosophy neatly: "A reasonable biogeographer is neither a vicarist nor a dispersalist but an eclecticist."

This study uses some cladistic biogeographic methods, although problems exist with the methodology, as follows: 1) possible errors in the character cladogram could result in errors in the taxon-area cladogram; 2) the method cannot positively distinguish between vicariance and concordant dispersal; 3) geological hypotheses are narratives, but they must be in geographic cladogram form to be easily compared with taxon-area cladograms; 4) the method acknowledges the utility of fossils but sometimes downplays their importance; 5) as used by some authors, the method is two-dimensional in its thinking, that is, the vertical displacements of land masses or ocean levels are often ignored; 6) the method is based on comparisons of groups of three or more endemic taxa; it de-emphasizes widespread taxa (which are used at a different level in the hierarchy in a manner analogous to the use of symplesiomorphies in a character cladogram); and 7) attempts to find congruent vicariant patterns require character cladograms for many different taxa, and these simply have not yet been constructed.

### METHODS

Organization of this study is as follows: 1) the geographic distribution patterns among and within corallanid genera (particularly endemism) are considered; and 2) a general descriptive synthesis of corallanid isopod distributions is made, with hypotheses to explain those distributions in light of cladistic analyses, geologic history, and other data.

This study uses cladistic biogeographic methods, wherein a character cladogram of corallanid genera is used to construct a taxon-area cladogram for comparison to a geographic cladogram. The methods used largely follow those detailed in the recent texts by Eldredge and Cracraft (1980), Nelson and Platnick (1981), Wiley (1981), and Humphries and Parenti (1986) and use the hypothetico-deductive method primarily as discussed by Morse and White (1979) and Brusca (1984), where "no paradigm is assumed to be of overriding importance, but rather an attempt is made to interpret the patterns of characters and the geographic distributions of taxa in the most biologically parsimonious fashion" (Brusca, 1984:102).

#### Distribution Maps

The distribution maps of corallanid genera are based upon specimens I examined (see taxonomy section for complete list) and upon those reported in the literature. Map localities were plotted as accurately as possible, but the diameter of the symbols used to indicate species localities covers a radius of approximately 100–200 km on the maps. Usually, no attempt was made to verify identifications or locality records taken from the literature unless there was some reason to doubt their validity (e.g. suspicious presence or absence of a particular taxon from an area).

#### Terminology

Lithospheric plate designations and plate boundaries are from the maps in Springer (1982). Abbreviations for lithospheric plates and for world oceans are noted in the various tables in which they appear.

Table 5. Number and percent of corallanid species found in various world oceans.*

| Isopod genus | Ocean<br>EP | WP | EI | WI | EA | WA |
|---|---|---|---|---|---|---|
| *Alcirona* | 2/33 | 5/83 | 1/17 | 0/0 | 1/17 | 1/17 |
| *Argathona* | 0/0 | 10/83 | 3/25 | 4/33 | 0/0 | 0/0 |
| *Corallana* | 0/0 | 13/81 | 2/13 | 5/31 | 0/0 | 0/0 |
| *Excorallana* | 5/25 | 0/0 | 0/0 | 0/0 | 1/5 | 15/75 |
| *Lanocira* | 1/13 | 3/38 | 3/38 | 6/75 | 0/0 | 2/25 |
| *Tachaea* | 0/0 | 5/83 | 2/33 | 0/0 | 0/0 | 0/0 |
| *Tridentella* (Tridentellidae) | 4/31 | 7/54 | 0/0 | 0/0 | 0/0 | 2/15 |

* EP = East Pacific, WP = West Pacific, EI = East Indian, WI = West Indian, EA = East Atlantic, WA = West Atlantic. Number of species reported is followed by percent of total species per genus (rounded to nearest whole number). Note that percentages may add up to >100% because some species are found in more than one ocean region.

In the following discussion, a distinction is made between species occurring in an ocean area and species occurring in the waters over a lithospheric plate.

### Taxon-Area Cladograms

These were constructed by placing the geographic (ocean) area occupied by a taxon in place of the taxon name on the cladogram resulting from the cladistic analysis (Fig. 39). Simplified (reduced) taxon-area cladograms were made by deleting unique, noncongruent areas from three-taxon statements in the area cladograms. These reduced taxon-area cladograms were compared to a geographic cladogram of ocean areas for congruence.

### Geographic Cladogram

This was constructed from the scenarios of earth history found in Dietz and Holden (1970), Briden and Smith (1977), Hallam (1981), Barron (1987), and others.

## RESULTS AND DISCUSSION

### Distribution of the Corallanidae

The Corallanidae are primarily a tropical/subtropical family of shallow-water isopods. The geographic distributions of species within each genus are shown on the maps in Figures 6, 10, 16, 25, 32, and 38 and Table 5. The number of endemic species per genus and percent of total species per genus found in various ocean regions are given in Table 6. All the genera except *Excorallana* attain their highest species diversity in the Indo-West Pacific region (Table 5). *Excorallana* is generally restricted to the New World, with 70% of its species endemic to the West Atlantic and 25% endemic to the East Pacific. *Argathona, Corallana,* and *Tachaea* are restricted to the Indo-West Pacific. The two remaining genera, *Alcirona* and *Lanocira,* are almost circumtropical in distribution, with only two to three species in each genus occurring in the New World.

Two species are known from both the Caribbean and the East Atlantic (*Alcirona krebsii* in Lineage A and *Excorallana oculata* in Lineage B). These are the only records of corallanids from the East Atlantic and probably represent either a simple dispersal from the New World or a reduced element of a West Atlantic–East Atlantic generalized track.

Table 7 shows that the majority of mobile animal hosts used by corallanid genera are fish, but turtles, shrimp, and scyphozoans have also been exploited as temporary hosts. Although this type of association is limited in duration, the possibility exists that some dispersals may have occurred via such "hosts."

The sister-group to the Corallanidae is the monogeneric Tridentellidae (*Tridentella*), which has 11 species, is found in tropical, temperate, and cold-temperature waters and is known from the West Atlantic, East Pacific, West Pacific, and Northwest Pacific. The other family used in the cladistic analysis, the Cirolanidae, is circumoceanic in distribution.

### Biogeographic Relationships of Sister-Groups

Two clear areas of corallanid endemism are evident in the taxon-area cladogram (Fig. 40) and in Table 6, corresponding to the Indo-West Pacific (Old World) and the West Atlantic–East Pacific (New World). Both corallanid lineages have some genera present in each of these areas of endemism.

In Lineage A, both *Alcirona* and *Lanocira* are represented in the New World (East Pacific and West Atlantic) by two to three species each, although each of these genera attains its highest species diversity in the Indo-West Pacific. The third Lineage A genus, *Argathona,* is endemic to the Indo-West Pacific. Lineage A contains relatively fewer species (25) than Lineage B (42) but is much more widely distributed, with all of its genera being exclusively marine. *Lanocira* and *Alcirona* are each present in five different ocean regions, and *Argathona* in three ocean areas (Tables 5, 6). *Alcirona* and *Lanocira* share West Atlantic, East Pacific, and West Pacific

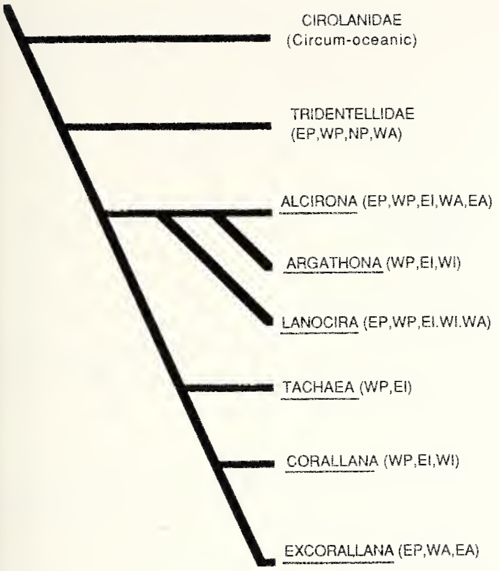

**Figure 40.** Taxon-area cladogram for the genera of Corallanidae.

areas with the sister-group Tridentellidae. *Argathona,* the endemic in Lineage A, shares West Pacific and Indian Ocean areas with each of the other two genera.

In Lineage B, *Tachaea* and *Corallana* are both endemic to the Indo-West Pacific, and *Excorallana* is primarily restricted to the New World. Lineage B is more speciose than Lineage A, with more species in "specialized," non-marine habitats. *Tachaea* is known mainly from freshwater ponds, lakes, and streams (as temporary parasites of certain shrimp and fish species—see Table 7). *Corallana* has 40% of its species described from estuarine or brackish habitats, many with wood-boring habits. One *Excorallana* species, *E. berbicensis,* has been reported from freshwater (Rio Berbice). Lineage B is more geographically restricted than Lineage A. *Tachaea* and *Corallana* are found in two or three areas in the Old World, and *Excorallana* in two ocean regions in the New World (excluding one species known from the East Atlantic, see above). *Corallana* and *Tachaea* share West Pacific and Indian Ocean areas, while *Excorallana* shares the East Pacific and West Atlantic areas with the sister-group Tridentellidae and the two widely distributed genera of Lineage A (Fig. 40).

## Comparison of Taxon-Area and Ocean-Formation Cladograms

Hypothesized relationships of ocean areas are depicted in Figure 41, a proposed cladogram of tropical ocean areas. This cladogram has somewhat ambiguous dates for earth history events, reflecting the controversy surrounding the dating of the various geotectonic events, as discussed by Dietz and Holden (1970), Briden and Smith (1977), Hallam (1981), Barron (1987), and others.

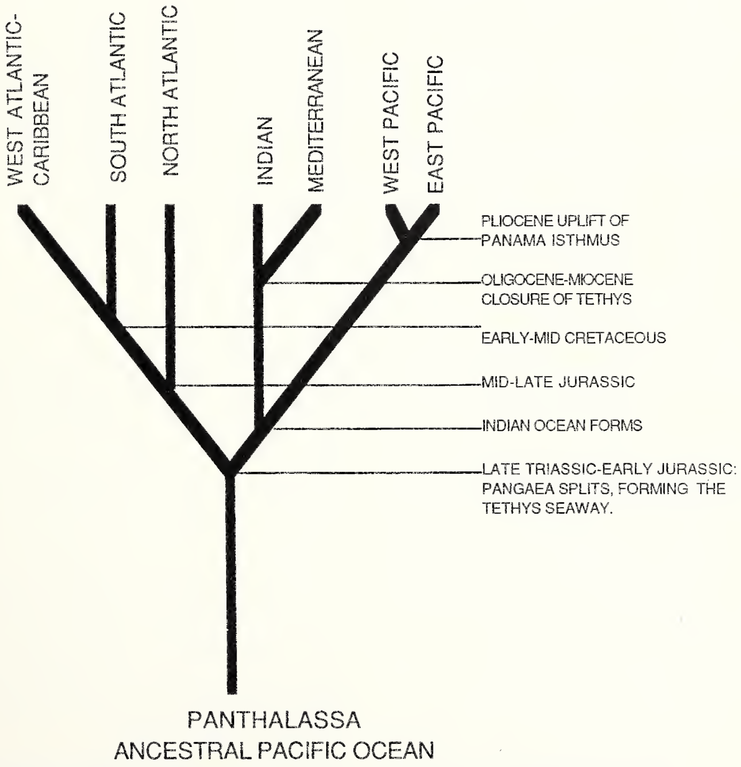

**Figure 41.** Proposed geographic cladogram depicting the opening of the tropical oceans.

Table 6. **Number and percent of corallanid species endemic to various world oceans.***

| Isopod genus | EP | WP | EI | WI | I | WA |
|---|---|---|---|---|---|---|
| *Alcirona* | 1/17 | 3/50 | 0/0 | 0/0 | 0/0 | 0/0 |
| *Argathona* | 0/0 | 8/67 | 0/0 | 1/8 | 2/17 | 0/0 |
| *Corallana* | 0/0 | 10/63 | 1/6 | 2/13 | 3/19 | 0/0 |
| *Excorallana* | 5/25 | 0/0 | 0/0 | 0/0 | 0/0 | 14/70 |
| *Lanocira* | 0/0 | 0/0 | 0/0 | 3/38 | 3/38 | 2/25 |
| *Tachaea* | 0/0 | 4/67 | 1/17 | 0/0 | 1/17 | 0/0 |
| *Tridentella* (Tridentellidae) | 4/31 | 7/54 | 0/0 | 0/0 | 0/0 | 2/15 |

* EP = East Pacific, WP = West Pacific, EI = East Indian, WI = West Indian, I = Indian (total), WA = West Atlantic. Number of endemic species is followed by percent species per genus (rounded to nearest whole number). Note that percentages may add up to >100% because some ocean regions include smaller ocean regions.

Limited congruence exists between the simplified (reduced) taxon-area cladogram (Fig. 42A) and the reduced geographic cladogram of tropical ocean areas (Fig. 42B). The fact that both corallanid lineages share Pacific, Atlantic, and Indian Ocean areas, while the sister-group Tridentellidae shares only Pacific and Atlantic Ocean areas, was taken as support for the hypothesis that the divergence of the Corallanidae and the Tridentellidae was related to the opening of the Indian and Atlantic Oceans.

Of the later events pictured on the geographic cladogram, the opening of the North and South Atlantic Oceans can be excluded from the analysis. Corallanids are not known from these areas. The remaining events on the cladogram are those involving paleo-epicontinental seas, the closure of Tethys (creating the Mediterranean), and the uplift of the Panamanian isthmus.

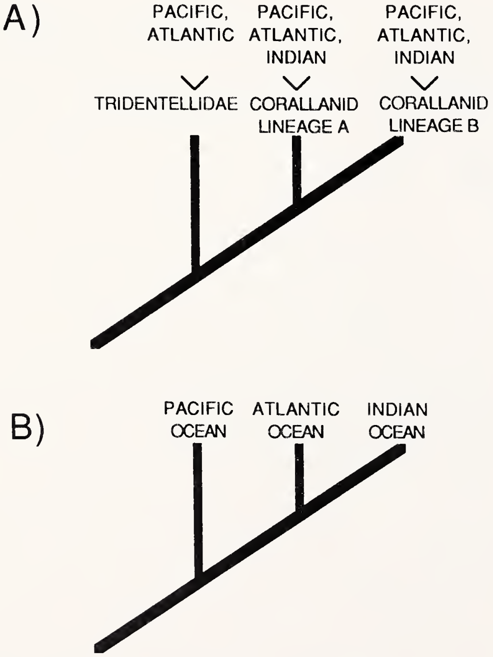

**Figure 42.** **A**, Reduced taxon-area cladogram for the Corallanidae. **B**, Reduced geographic cladogram of tropical oceans.

## Phylogeny of the Corallanidae

This scenario is based on the above comparison of the taxon-area cladogram and ocean-formation cladogram, as well as other biological data.

The taxa cladogram resulting from cladistic analysis (Fig. 39) is interpreted as depicting the Corallanidae and Tridentellidae evolving from some common ancestral "cirolanoid-like" stock and also indicates two lineages within the Corallanidae. Lineage A consists of *Alcirona, Argathona,* and *Lanocira* and Lineage B includes *Tachaea, Corallana,* and *Excorallana.*

It may be hypothesized that the modern genera within the Tridentellidae and Corallanidae evolved from common ancestors present in Panthalassa (the ancestral Pacific Ocean) or later in the cosmopolitan warm-water Tethyan biota discussed by Brusca (1984) and Hallam (1981). There is evidence for the progressive divergence of some elements of the Tethyan fauna, such as rudistid bivalves and large benthic foraminiferans between the Caribbean and Mediterranean regions (Coates, 1973; Kauffman, 1973). Heck and McCoy (1976) claimed that the modern distributions of corals, seagrasses, seagrass-associated foraminiferans, and mangroves support the concept that a circumglobal Tethyan-track fauna existed at one time. The distribution of modern circumtropical coastal faunas, including the Corallanidae, can be hypothesized to be due at least partially to the fragmentation of this tropical Tethyan track.

Divergence of the Corallanidae from the Tridentellidae was probably related to the opening of the Atlantic and Indian Oceans in the late Triassic or early Jurassic (Fig. 43). This would explain the fact that *Lanocira* attains its highest species diversity in the Indian Ocean, as well as being one of the older, widely distributed genera.

The two lineages within the Corallanidae must have diverged from each other prior to the closure

Table 7. Genera of temporary hosts for corallanid isopod genera.*

| Isopod genus | Temporary host genus | Family |
|---|---|---|
| *Alcirona* | *Pseudoscarus* | Scaridae |
| | *Priacanthus* | Priacanthidae |
| | *Scarus* | Scaridae |
| | *Echidna* | Muraenidae |
| | *Amphacanthus* | Acanthuridae |
| *Argathona* | *Epinephelus* | Serranidae |
| | *Diagramma* | Serranidae |
| | *Pseudolabras* | Labridae |
| | *Cromileptes* | Serranidae |
| | *Lutjanus* | Lutjanidae |
| | *Plectropomus* | Serranidae |
| | *Tetraodon* | Tetraodontidae |
| | *Variola* | Serranidae |
| | *Muraena* | Muraenidae |
| | *Chelonia* (turtle) | |
| *Corallana* | *Chanos* | Chanidae |
| | *Puntius* | Cyprinidae |
| *Excorallana* | *Mycteroperca* | Serranidae |
| | *Epinephelus* | Serranidae |
| | *Priacanthus* | Priacanthidae |
| | *Lachnolaimus* | Labridae |
| | *Ocyurus* | Lutjanidae |
| | *Sparisoma* | Scaridae |
| | *Neomaenis* | Lutjanidae |
| | *Caranx* | Carangidae |
| | *Haemulon* | Pomadasyidae |
| | *Sphyraena* | Sphyraenidae |
| | *Scarus* | Scaridae |
| | *Diodon* | Diodontidae |
| | *Aetobatus* | Myliobatididae |
| | *Dasyatis* | Dasyatididae |
| | *Lycengraulis* | Engraulidae |
| | *Chelonia* (turtle) | |
| *Lanocira* | *Cassiopea* (scyphozoan) | |
| | *Variola* | Serranidae |
| *Tachaea* | *Culter* | Cyprinidae |
| | *Caridina* (shrimp) | |
| | *Palaemon* (shrimp) | |
| | *Palaemonetes* (shrimp) | |
| | *Paratya* (shrimp) | |
| | *Leander* (shrimp) | |
| | *Macrobrachium* (shrimp) | |

* Mobile animal hosts only; all temporary host genera listed are fish except as indicated in parentheses; family names given for fish genera only. Records were taken from specimen labels or from the literature.

of the Tethys seaway at its eastern end, in the late Oligocene or early Miocene, because both Old World (Indo-West Pacific) and New World (East Pacific–West Atlantic) endemic genera are present in Lineage B. To assume otherwise requires invoking multiple dispersals, either across the Pacific Ocean or through nontropical waters; neither of these possibilities is convincingly supported by corallanid distribution patterns.

Eustatic transgression and regression of epicontinental seaways separating Asia and Europe in the late Jurassic and North America in the mid-Cretaceous (Kauffman, 1973; Cox, 1974; Hallam, 1981) may also have contributed to the divergence of these lineages by allowing Lineage B to exploit new habitats. Lineage A is exclusively marine, has two genera that are almost circumtropical, and has the least derived morphology; whereas Lineage B, with three endemic genera, has two genera that have exploited brackish, estuarine, and freshwater habitats, and shows the most derived states of the Corallanidae's character transitions towards reduction and simplification of appendages.

The existence of East Pacific–West Atlantic geminate species in *Excorallana* (see Delaney, 1984) indicates that modern corallanid genera probably

**Table 8. Number of corallanid species endemic to various lithospheric plates.***

| Isopod genus | Lithospheric plate | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | P | N | C | NA | A | IA | E | PH | AR | CO | SA |
| *Alcirona* | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 |
| *Argathona* | 0 | 0 | 0 | 0 | 0 | 5 | 3 | 1 | 0 | 0 | 0 |
| *Corallana* | 0 | 0 | 0 | 0 | 1 | 7 | 3 | 1 | 0 | 0 | 0 |
| *Excorallana* | 1 | 1 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| *Lanocira* | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Tachaea* | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 |
| *Tridentella* (Tridentellidae) | 4 | 2 | 0 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |

* Lithospheric plates (after Springer, 1982) are designated as follows: P = Pacific, N = Nazca, C = Caribbean, NA = North American, A = African, IA = Indian-Australian, E = Eurasian, PH = Philippine, AR = Arabian, CO = Cocos, SA = South American. Two *Tridentella* species from New Zealand are not included above, because they are considered to be on two lithospheric plates (IA and P).

existed prior to the Pliocene. These geminates are still identifiable despite the passage of millions of years since the Pliocene uplift of the Central American isthmus. This may indicate a relative speciation rate for corallanid isopods.

The pre-Pliocene existence of corallanid genera, together with the limited congruence between the reduced cladograms (Figs. 42A, B), establishes a relative timescale for divergence of modern genera within Lineage B. These genera probably diverged after Tethys closure in the late Oligocene or early Miocene, but prior to the Pliocene. It is hypothesized that the closure of Tethys was associated with the divergence of *Excorallana* and *Corallana*. These

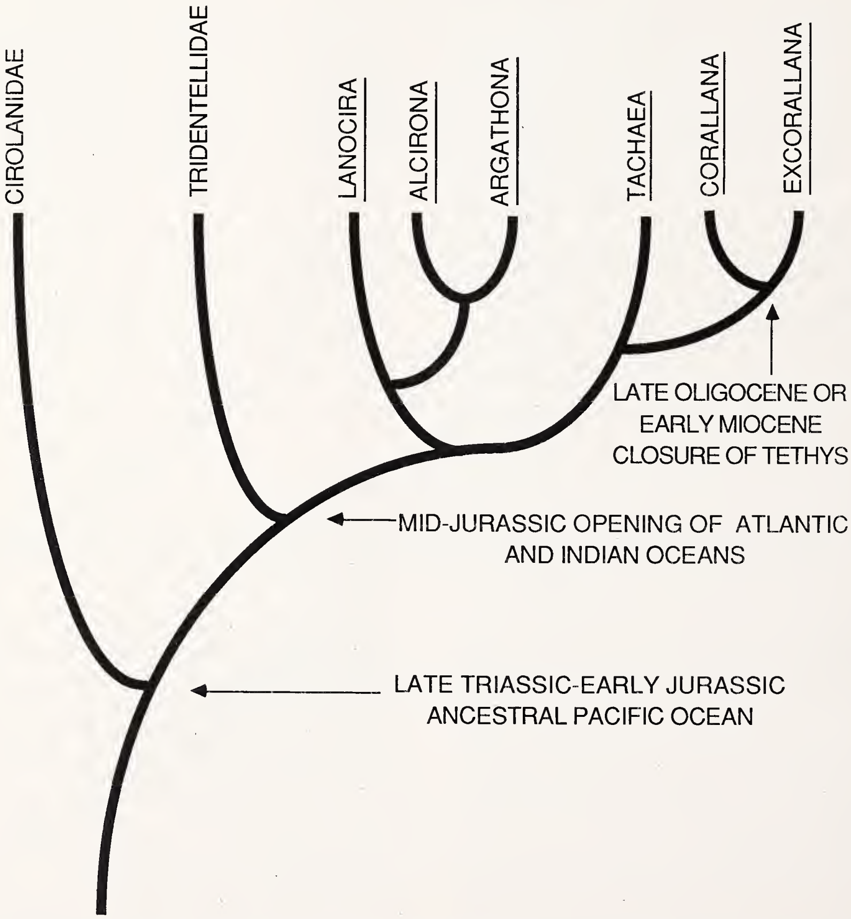
CIROLANIDAE
TRIDENTELLIDAE
LANOCIRA
ALCIRONA
ARGATHONA
TACHAEA
CORALLANA
EXCORALLANA
LATE OLIGOCENE OR EARLY MIOCENE CLOSURE OF TETHYS
MID-JURASSIC OPENING OF ATLANTIC AND INDIAN OCEANS
LATE TRIASSIC-EARLY JURASSIC ANCESTRAL PACIFIC OCEAN

**Figure 43.** Proposed phylogeny for the genera of Corallanidae, derived from Figures 40–42 and other data.

genera are sister-groups (Fig. 39), yet are restricted to the New and Old Worlds, respectively.

Table 8 indicates the affinities of corallanid and tridentellid species to various lithospheric plates. Note that corallanid genera are only marginally represented on the Pacific plate, in contrast to shorefishes and some invertebrate taxa (Springer, 1982); there are no corallanid genera endemic to the Pacific plate, and only one endemic corallanid species. Although more corallanid species doubtlessly will be described from the vast Pacific area, the paucity of species from the Pacific plate leads one to dismiss use of the two alternate geotectonic theories of earth evolution, "Pacifica" (Nur and Ben-Avraham, 1977; Ben-Avraham, 1981) and "earth expansion" (Carey, 1976, 1983; Pitman et al., 1974). Both of these theories would require distributions of corallanid isopods in and around the Pacific Basin that are unsupported by collection data or would require multiple dispersals to explain present distributions. The classic continental drift and plate tectonic theories (Dietz and Holden, 1970; Briden and Smith, 1977; Hallam, 1981; Barron et al., 1987; and others) are more parsimonious than other earth history theories in explaining the phylogeny of the Corallanidae (Fig. 43).

Paleontological records of isopods are relatively scarce; fossil flabelliferans are known from the Triassic of Germany, Jurassic of Britain and Central Europe, and Cretaceous of Brazil (Schram, 1986: 151). Many flabelliferan families are distinguished by appendage morphology, which is usually poorly preserved in isopod fossils. Thus, there are no fossil corallanids or tridentellids known that might corroborate either out-group or biogeographic relations.

Various physical and biological processes were responsible for the evolution of the Corallanidae and for the biogeographic distributions of its genera. Vicariant events were influenced by physical processes resulting from geotectonic, eustatic, paleoclimatic, and oceanographic conditions. Biological factors included dispersals, extinctions, and developmental mode. The evolutionary effect of these processes on the Corallanidae has apparently been: 1) the development of "temporary parasitism," 2) the adaptation of appendages toward an increasingly parasitic lifestyle, and 3) the ecological radiation of corallanid genera in marine, brackish, and freshwater habitats.

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## APPENDIX I: INVALID CORALLANID NAMES

### INVALID CORALLANID GENUS NAMES

*Austroargathona* Riek, 1953 (now *Tachaea*)
*Brotherus* Budde-Lund, 1908 (now *Argathona*)
*Gurida* Budde-Lund, 1908 (now *Argathona*)
*Icochaea* Caldwell, 1879 (*lapsus*) (now *Tachaea*)
*Icochaes* Shen, 1936 (now *Tachaea*)
*Nalicora* Moore, 1902 (now *Lanocira*)
*Orcilana* Nierstrasz, 1931 (now *Argathona*)

### INVALID CORALLANID SPECIES NAMES

*Alcirona hirsuta* Moore, 1902 (now *Alcirona krebsii*)
*Alcirona insularis* Hansen, 1890 (now *Alcirona krebsii*)
*Alcirona macronema* (Bleeker, 1857) (now *Argathona macronema*)
*Alcirona maldivensis* Stebbing, 1904 (now *Alcirona krebsii*)
*Alcirona pearsoni* Monod, 1926 (now *Argathona rhinoceros*)
*Alcirona tuberculata* Richardson, 1910 (now *Cirolana tuberculata*)

*Argathona longicornis* (Budde-Lund, 1908) (now *Argathona macronema*)
*Argathona reidi* Stebbing, 1910 (now *Argathona rhinoceros*)
*Argathona similis* Richardson, 1910 (now *Argathona macronema*)
*Austroargathona caridophaga* Riek, 1953 (now *Tachaea caridophaga*)
*Austroargathona picta* Riek, 1967 (now *Tachaea picta*)
*Brotherus longicornis* Budde-Lund, 1908 (now *Argathona macronema*)
*Corallana acuticauda* Miers, 1881 (now *Excorallana acuticauda*)
*Corallana antillensis* Hansen, 1890 (now *Excorallana acuticauda*)
*Corallana fissicauda* Hansen, 1890 (now *Excorallana fissicauda*)
*Corallana macronema* Miers, 1881 (now *Argathona macronema*)
*Corallana mexicana* Nierstrasz, 1917 (now *Excorallana mexicana*)
*Corallana oculata* Hansen, 1890 (now *Excorallana oculata*)
*Corallana quadricornis* Hansen, 1890 (now *Excorallana quadricornis*)
*Corallana sexticornis* Richardson, 1901 (now *Excorallana sexticornis*)
*Corallana subtilis* Hansen, 1890 (now *Excorallana subtilis*)
*Corallana tricornis* Hansen, 1890 (now *Excorallana tricornis tricornis*)
*Corallana truncata* Richardson, 1899 (now *Excorallana truncata*)
*Corallana warmingii* Hansen, 1890 (now *Excorallana warmingii*)
*Excorallana antillensis* Lemos de Castro, 1960 (now *Excorallana acuticauda*)
*Excorallana kathyae* Menzies, 1962 (now *Excorallana truncata*)
*Excorallana rapax* Schultz, 1969 (now *Lanocira rapax*)
*Gurida coelata* Budde-Lund, 1908 (now *Argathona rhinoceros*)
*Icochaes crassipes* Shen, 1936 (now *Tachaea crassipes*)
*Lanocira capensis* Barnard, 1914 (now *Lanocira gardineri*)
*Lanocira hirsuta* Nordenstam, 1930 (now *Lanocira zeylanica*)
*Nalicora rapax* Moore, 1902 (now *Lanocira rapax*)
*Orcilana hanseni* Nierstrasz, 1931 (now *Argathona macronema*)
*Tachaea incerta* Hansen, 1890 (now *Tachaea crassipes*)
*Tachaea leopoldi* Nierstrasz, 1930 (now *Corallana leopoldi*)

## APPENDIX II: CHARACTERS USED IN THE CLADISTIC ANALYSIS

Multistate characters used in this analysis follow, with alphanumeric designations, the character state descriptions, and the numeric code assigned to each state.

1) a—Mandible incisor short (0)
   b—Mandible incisor short or long (1)
   c—Mandible incisor long (2)
2) a—Mandible molar process large, robustly spined (0)
   b—Mandible molar process reduced (in spination and/or size) or absent (1)
3) a—Mandible with robust lacinia mobilis (0)
   b—Mandible with small lacinia mobilis (1)
   c—Mandible without lacinia mobilis (2)
4) Maxillule lateral lobe apex:
   a—with 11–14 spines (0)
   b—with 3–5 stout hooked spines and smaller subapical spines (1)
   c—with 2 large falcate spines, 0–3 smaller spines between them (2)
   d—with 1 large falcate spine, and with 1–3 hooklike subapical spines (3)
   e—with 1 large falcate spine only (4)
5) Maxillule medial lobe:
   a—with 3–4 robust, circumplumose spines (0)
   b—with simple apex, without robust plumose spines (1)
6) Maxilla:
   a—with medial and lateral lobes (0)
   b—uniramous, stout, 2-articulate, with conical apex (1)
   c—uniramous, short, rounded lobe (2)
   d—uniramous, with apex bi- or trilobed (3)
   e—uniramous, 3–4-articulate, apical article sublinear and elongate (4)
7) Maxilliped palp:
   a—5-articulate (0)
   b—4- or 5-articulate (1)
   c—3- or 5-articulate (2)
8) Maxilliped basis:
   a—forming an endite (0)
   b—not forming an endite (1)
9) Maxilliped palp middle article:
   a—not elongate (0)
   b—elongate (1)
10) Maxilliped basis:
   a—not elongate (0)
   b—elongate (1)
   c—basis very elongate, maxilliped slender (2)
11) Mandible:
   a—without row of denticles behind incisor (0)
   b—with row of denticles behind incisor (1)
12) Antennule peduncle:
   a—3-articulate (0)
   b—2–3-articulate (1)
   c—2-articulate (2)
13) Antennule peduncle:
   a—basal article not expanded (0)
   b—basal article expanded (1)
14) Pereopod I carpus:
   a—inner angle not produced (0)
   b—inner angle produced (1)
15) Pereopod I dactylus:
   a—without serrated margin (0)
   b—with serrated margin (in some species) (1)
16) Eyes:
   a—not divided by unpigmented, transverse band (0)
   b—divided by unpigmented, transverse band (in some species) (1)
17) Frontal lamina:

a—present, not reduced (0)
b—occasionally reduced or absent (1)

18) Pleotelson:
a—without lateral incisions (0)
b—with lateral incisions (in some species) (1)

19) Frontal lamina:
a—always flat, not projecting (0)
b—projecting ventrally in some species (1)

20) Maxilla apex:
a—without dentate, scalelike spines (0)
b—with dentate, scalelike spines (1)

21) Maxillule medial lobe:
a—apex simple in shape, rounded or narrow (0)
b—apex truncate and expended distally (1)

## APPENDIX III: DATA MATRICES USED IN PAUP AND PHYLIP

PAUP:

| Taxa | Characters 1–21 |
|---|---|
| *Corallana* | 1 1 1 4 1 2 0 1 0 2 0 1 1 0 0 0 1 0 0 0 0 |
| *Alcirona* | 0 1 2 2 1 2 0 1 0 0 0 2 0 0 1 0 0 0 0 0 1 |
| *Argathona* | 0 1 2 3 1 2 1 1 0 0 0 2 0 0 1 1 0 0 0 0 1 |
| *Lanocira* | 0 1 2 4 1 4 0 1 0 0 1 2 0 0 1 0 0 0 0 0 0 |
| *Excorallana* | 2 1 1 4 1 3 0 1 1 0 0 1 1 0 0 0 0 1 0 0 0 |
| *Tachaea* | 0 1 1 4 1 2 2 1 0 1 0 2 1 1 0 0 0 0 0 0 0 |
| Tridentellidae | 0 1 2 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 |
| Cirolanidae | 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 |

PHYLIP:

| Taxa | Characters 1–32 |
|---|---|
| *Alcirona* | 0 0 1 1 1 1 1 0 0 1 1 1 0 0 0 0 1 0 0 0 0 1 1 0 0 1 0 0 0 0 |
| *Argathona* | 0 0 1 1 1 1 1 1 0 1 1 1 0 0 1 0 1 0 0 0 0 1 1 0 0 1 1 0 0 0 |
| *Corallana* | 1 0 1 1 0 1 1 1 1 1 1 1 0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 1 0 0 |
| *Excorallana* | 1 1 1 1 0 1 1 1 1 1 1 1 1 0 0 0 1 1 0 0 0 1 0 1 0 0 0 0 1 0 |
| *Lanocira* | 0 0 1 1 1 1 1 1 1 1 1 1 1 1 0 0 1 0 0 0 1 1 1 0 0 1 0 0 0 0 |
| *Tachaea* | 0 0 1 1 0 1 1 1 1 1 1 1 0 0 1 1 1 0 1 0 0 1 1 1 1 0 0 0 0 0 |
| Tridentellidae | 0 0 1 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 |
| Cirolanidae | 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 |

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## New Evidence for the Age of the South Mountain Local Fauna, Ventura County, California

Mark A. Mason and Carl C. Swisher III

Natural History Museum of Los Angeles County

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# NEW EVIDENCE FOR THE AGE OF THE SOUTH MOUNTAIN LOCAL FAUNA, VENTURA COUNTY, CALIFORNIA

MARK A. MASON[1] AND CARL C. SWISHER III[2]

**ABSTRACT.** The South Mountain Local Fauna is a small assemblage of fossil vertebrates from the uppermost beds of the Sespe Formation in Ventura County, California, U.S.A. The remains of mammals have been found in a variegated interval of sandstones and mudstones. Vertebrate fossils have been collected from within an interval of about 638 m (2100 ft.). Included in this local fauna is the oreodont *Sespia californica* (Stock, 1930), which has affinities with *S. marianae* Schultz and Falkenbach, 1948, from the lowest part of the Arikaree Group of Nebraska.

A $^{40}$K-$^{40}$Ar age of 28.2 ± 0.2 Ma (weighted average of two analyses) was obtained on biotite from the Willard Canyon tuff, a pumiceous bed that lies about 271 m stratigraphically below the top of the Sespe Formation at South Mountain. Because previous work in Nebraska has yielded similar isotopic ages, both of the mentioned species of *Sespia* are now closely tied to dates of about 28 Ma. These data support the faunal correlation and land mammal age assignment of Arikareean for the South Mountain Local Fauna. The age determination for the Willard Canyon tuff reaffirms an approximate 28 to 29 Ma age for the earliest Arikareean.

The South Mountain Local Fauna is overlain by a "Vaqueros" Stage molluscan assemblage from the Vaqueros Formation. The Zemorrian–Saucesian Pacific Coast benthic foraminiferal stage boundary is approximately coincident and has been dated at 22 to 23 Ma, thus providing a minimum age for the Sespe–Vaqueros contact at South Mountain.

A specimen referable to *Sespia* has been collected from South Mountain at a stratigraphically higher level than previously reported material of this taxon.

The Alamos Canyon Local Fauna near Big Mountain is not younger than early Arikareean due to the constraints imposed by overlying "Vaqueros" Stage mollusks and early Saucesian (late Zemorrian?) foraminifera.

## INTRODUCTION

The Sespe Formation is a thick, predominantly nonmarine, clastic unit that is widely exposed in the northern Peninsular and southern Transverse Ranges of southern California (Fig. 1). At South Mountain, south of Santa Paula in Ventura County, approximately 638 m (2100 ft.) of the upper part of the Sespe Formation are exposed along the north flank of the South Mountain–Oak Ridge anticline. The total stratigraphic thickness of the Sespe in the vicinity of South Mountain is about 1800 to 2100 m (6000 to 7000 ft.) as determined from well-core data obtained from oil wells in the South Mountain Field (Stock, 1930; Baddley, 1954). The lithology is characterized by alternating variegated sandstones and red mudstones. A single tuffaceous mudstone also lies within the upper part of the South Mountain section. The Sespe Formation at South Mountain is unconformably overlain by the marine Vaqueros Formation as it is elsewhere in the Ventura Basin (Stock, 1930; Yeats, 1987).

Fossil vertebrates that have been collected from the Sespe Formation within the Ventura Basin suggest a range of North American Land Mammal Age (NALMA) assignments of Uintan to Arikareean (Stock, 1948). The steep badland exposures of the Sespe Formation at South Mountain have produced a small fossil vertebrate sample from the uppermost beds (Figs. 1 and 2). Among the taxa reported from this area is the holotype of *Sespia californica* (Stock, 1930), which is noteworthy for being one of the taxa that characterize the early Arikareean NALMA. Stock (1930, 1934) and Wilson (1949) are the primary authorities for description of the South Mountain Local Fauna. Previous discussions of the systematic and temporal implications for the South Mountain Local Fauna have been presented by Schultz and Falkenbach (1949, 1954, 1968), Durham *et al.* (1954), Stirton (1960), and Savage and Russell (1983). Stirton (1960) has provided the most recent faunal list and suggested marine correlations.

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[1] Museum of Paleontology, University of California, Berkeley, California 94720.

[2] Berkeley Geochronology Center, 2453 Ridge Road, Berkeley, California 94709.

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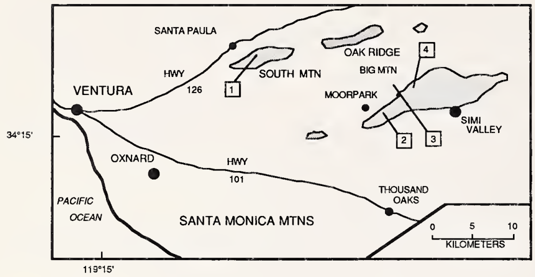

**Figure 1.** Index map of the southern portion of Ventura County, California, with fossil localities and major outcrops of the Sespe Formation indicated. Dot pattern represents major Sespe outcrops. Locality numbers are as follows: 1) South Mountain Local Fauna; 2) "Moorpark leptauchenid"; 3) Big Mountain marine invertebrate localities; 4) Alamos Canyon Local Fauna.

## MATERIALS AND METHODS

### $^{40}$K-$^{40}$Ar ANALYSES

A sample of the Willard Canyon tuff was collected for analysis at the Berkeley Geochronology Center. The sample was crushed, sized, and ball-milled to remove attached devitrified glass, and then the biotite was separated from the glass using a Frantz magnetic separator. The resultant biotite separate contained about 20 percent oxidized biotite grains. The altered biotite grains were removed from the fresher, dark-looking grains using an MEI (heavy liquid) density column. The biotite was then put in a distilled water bath in an ultrasonic cleaner to remove any remaining attached devitrified glass.

Argon isotope abundances of gas extracted after total fusion of sample splits were measured on Reynolds-type rare-gas mass spectrometers using isotope dilution by calibrated $^{38}$Ar spikes, metered from a pipette system.

Age reduction and calculation of errors were made with an on-line Macintosh computer. The $^{38}$Ar calibration was established by control dates on in-house standards JFE 64-29 and GHC305 and are calibrated in turn with interlaboratory standards of known age and by first principles using gas laws, atmospheric abundance and isotopic composition, and the assumption of the invariant volumes in the precisely manufactured air-pipette system.

Potassium analyses were made in duplicate on sample splits with a Zeiss PF-5 flame photometer following procedures described by Carmichael *et al.* (1968).

The one-sigma ($1\sigma$) errors that accompany each age analysis incorporate variation calculated in the measurement of 1) duplicate potassium measurements, 2) total $^{40}$Ar/$^{36}$Ar correction, 3) $^{36}$Ar/$^{38}$Ar spike composition, 4) $^{40}$Ar/$^{38}$Ar and $^{38}$Ar/$^{36}$Ar initial ratios, and 5) $^{38}$Ar spike calibration and are calculated using standard propagation of error methods.

The weighted average is calculated following procedures described in Taylor (1982).

Decay constants used in the age calculations are those recommended by Steiger and Jager (1977): Decay constants; $\lambda_\epsilon + \lambda_\epsilon' = 0.581 \times 10^{-10}\ \mathrm{yr}^{-1}$; $\lambda\beta = 4.962 \times 10^{-10}\ \mathrm{yr}^{-1}$; $^{40}$K/K total = $1.167 \times 10^{-4}$ mol/mol.

Where necessary, all of the isotopic age determinations cited in this paper have been corrected to the new constants of Steiger and Jager (1977).

## MEASUREMENTS AND ABBREVIATIONS

The methodology for measuring fossil specimens follows Schultz and Falkenbach (1968), and the values are expressed in millimeters. The dental dimensions have this convention: anteroposterior by buccolingual. Tooth measurements that are approximate due to damage are indicated with the symbol @. Additional abbreviations are: a-p, anteroposterior; b-l, buccolingual; ft., feet; m, meter(s); mm, millimeter(s); Ma, megannum; NALMA, North American Land Mammal Age.

## SYSTEMATIC PALEONTOLOGY

### Merycoidodontidae Hay, 1902

### *Sespia* sp., cf. *S. californica* (Stock, 1930)

**SPECIMEN.** LACM 5549, right and left paired dentaries with partial dentition; left $M_{2-3}$ fragments and right $P_3$–$M_3$ fragments.

**LOCALITY.** LACM (CIT) 300, Willard Canyon, South Mountain, Ventura County, California. Precise locality data are available to qualified professionals from the Natural History Museum of Los Angeles County.

**AGE AND HORIZON.** Arikareean; Sespe Formation; approximately 265 m (870 ft.) below the top of the Sespe.

**DESCRIPTION.** LACM 5549 is a pair of partial dentaries with worn right $P_4$–$M_3$ and worn and damaged left $M_{2-3}$. The occlusal surfaces are obliterated by extensive wear, yet some dental features may be observed. C: ovate alveolus, no diastema. $P_2$–$P_4$ single-rooted. The $P_4$ paracristid is subparallel to the midsagittal plane and is not sharply deflected from an anteroposterior orientation. $M_1$: quadratic in occlusal outline with buccal damage. Both anterior molars have lost the occlusal enamel and show the hypoflexid or median valley. $M_2$: heavily worn quadrate tooth that is significantly larger than $M_1$. $M_3$: significantly larger than $M_2$ and with a prominent hypoconulid. The mental foramina are situated ventral to $P_4$ and near the dorsoventral midpoint of the dentary. $P_1$–$P_4$ are single-rooted with elliptical alveoli. A partial ascending ramus is present.

**DISCUSSION.** This specimen closely approximates the conditions seen in other dentaries of *Sespia californica* (Stock), although the holotype has a smaller $M_3$ hypoconulid and the mental foramen is situated 0.5 mm more anteriorly compared to the holotype. Diagnostic characters include a gracile dentary with the postsymphysis at $P_3$, a deep horizontal ramus, and a high ascending ramus. The crowded and relatively small premolars contrast with the progressively elongate molars. Should further material from this level substantiate this species assignment, then *S. californica* has a stratigraphic range of about 608 to 265 m below the top of the Sespe Formation at South Mountain.

LACM 5549 retains the only ascending ramus known for any of the leptaucheniines from the Sespe Formation. It is damaged, but it appears to be as high as or higher than that found in *S. marianae* Schultz and Falkenbach, 1968. The southern Californian species is the more primitive of the two in its small size, less hypsodont cheek teeth, and relatively uncrowded premolars in comparison to *S. marianae.*

*Sespia californica* may be the older of the two species of *Sespia* because of its relative primitiveness and its stratigraphic range, which extends well below the Willard Canyon tuff at South Mountain, but the evidence remains inconclusive. There is nothing in the present analysis that eliminates the competing hypothesis that considers the two species geologically contemporaneous.

**MEASUREMENTS OF THE SPECIMEN.** $P_4$, 4.2 × 3.0 @; $M_1$, 4.5 × 3.5 @; $M_2$, 6.3 × 4.5 @; $M_3$, 13.0 × 4.8. The depth of the ramus at $M_3$ is 18.0 mm. The height of ascending ramus at the coronoid notch is estimated to be 40 mm. The length of $P_1$–$M_3$ is 38@ mm. The length $P_1$–$P_4$ is 14@ mm. The length $M_1$–$M_3$ is 23.5 mm.

Some remeasurements of the holotype of *Sespia californica* were found to differ from those published by Schultz and Falkenbach (1968) and are: depth of jaw at anterior edge of $M_3$, 17.0 mm and length $M_1$–$M_3$, 23.5@ mm.

## STRATIGRAPHY AND GEOCHRONOLOGY

Based primarily on the stage of evolution of the oreodonts at South Mountain, Stock (1930) considered the South Mountain Local Fauna to correlate with the fossil mammals from the lower "Rosebud" Formation of South Dakota. Wilson (1949) assigned the fauna from the upper 152 m (500 ft.) at South Mountain to the Arikareean NALMA and suggested an age range from Whitneyan to Arikareean for the lower 486 m (1600 ft.). Schultz and Falkenbach (1949, 1954, 1968) correlated the South Mountain Local Fauna with the upper Gering and Monroe Creek faunas of Nebraska. Stirton (1960), in a paper on a marine carnivore, discussed the age of the South Mountain Local Fauna and assigned it to the Arikareean. Savage and Russell (1983) have more recently recalled Wilson's (1949) interpretation and assigned only those fossil mammals from the upper part of the Sespe Formation (Willard Canyon sites) to the Arikareean. Tedford *et al.* (1987) have presented the most recent consensus opinion that the South Mountain Local Fauna is a correlate of the fauna from the Gering Formation of Nebraska.

Much of the controversy regarding the age of the South Mountain Local Fauna is due to the dearth of fossils that are encountered within the thick stratigraphic interval in this area. An oreodont described herein raises the known stratigraphic range of leptaucheniines in the South Mountain section about 61 m (200 ft.) from previous reports and demonstrates the uncertainty regarding the true stratigraphic ranges of the few reported taxa.

### WILLARD CANYON TUFF

A study directed toward collecting additional fossil vertebrates from the Sespe Formation at South Mountain resulted in the identification of a tuff about 271 m (890 ft.) below the Sespe–Vaqueros formational contact, 60 m (200 ft.) above the top of Stock's (1934) "Leptauchenid Zone," and about 337 m (1100 ft.) above the type locality of *Sespia californica.* Primary extrusive volcanic rocks are rare in the Sespe Formation and no previous isotopic age analyses have been reported in the literature. The Willard Canyon tuff, so named for the canyon with readily accessible and excellent exposures of this pumiceous tuff, has abundant euhedral biotite in a mudstone matrix as well as pebble to granule-sized, biotite-rich, pumice fragments.

Two argon analyses of the biotite (KA 5590R and 5590R-2), conducted at the Berkeley Geochronology Center, yielded 40.9 and 40.0 percent radiogenic argon, a K content of 6.12 percent for ages of 28.1 ± 0.3 Ma and 28.3 ± 0.37 Ma, respectively. An overall age of 28.2 ± 0.2 Ma (weighted average) is indicated for the Willard Canyon tuff (Table 1). The age of this tuff was erroneously reported as 27.8 Ma in an abstract by Mason and Swisher (1988).

### SESPE FORMATION–VAQUEROS FORMATION RELATIONSHIPS

Some discordant geochronologic correlations in the Ventura Basin are evident from the data presently available. The predominantly marine Vaqueros Formation of the Ventura Basin has produced marine megafossils and microfossils of chronologic significance. The marine megafaunas of the South Mountain and Big Mountain areas reported by Loel and Corey (1932) and Corey *in* Cushman and LeRoy (1938) contain *Turritella inezana* Conrad, 1857, *Rapana vaquerosensis* Arnold, 1907, and *Macrochlamys magnolia* (Conrad, 1857). In addition, there are taxa that are not shared by these two faunas. The South Mountain assemblage includes *Crassostrea eldridgei* (Arnold, 1907) and *Dosinia margaritana projecta* Loel and Corey, 1932, but the Big Mountain assemblage has only one restricted species—*Crassostrea vaquerosensis* (Loel and Corey, 1932). All range zones of these taxa are restricted to the "Vaqueros" provincial molluscan stage as provisionally defined by Addicott (1972), and the beds containing them are assigned accordingly. Addicott (1972) correlates the "Vaqueros" Stage with the late Zemorrian and early Saucesian Pacific Coast provincial benthic foraminiferal stages of Kleinpell (1938).

Table 1. **Data from $^{40}$K-$^{40}$Ar analyses of the Willard Canyon tuff, South Mountain, Ventura County, California.**

| Sample number | KA no. | Material dated | Weight (g) | % K (mean) | $^{40}$Ar* (mol/g) | $^{40}$Ar* (%) | Age (Ma ± 1σ) | Weighted mean (Ma) |
|---|---|---|---|---|---|---|---|---|
| 86SM1 | 5590R | Biotite | 0.26985 | 6.163 | $3.021^{-10}$ | 40.9 | 28.05 ± 0.30 | |
| | 5590R-2 | Biotite | 0.24477 | 6.163 | $3.053^{-10}$ | 40.0 | 28.34 ± 0.37 | 28.20 ± 0.2 |

Decay constants: $\lambda_\epsilon + \lambda_\epsilon' = 0.581 \times 10^{-10}$ yr$^{-1}$; $\lambda = 4.962 \times 10^{-10}$ yr$^{-1}$; $^{40}K/K_{total} = 1.167 \times 10^{-4}$.

* Radiogenic $^{40}$Ar.

Well-documented late Zemorrian and early Saucesian foraminifera from the Vaqueros Formation of the Big Mountain area provide a direct tie between the foraminiferal and marine molluscan chronostratigraphic disciplines, despite some well-recognized problems with diachronic benthic foraminiferal stage boundaries. The two subdivisions of the Zemorrian Stage (Kleinpell, 1938) have been refined by Tipton *et al.* (1973) and further refined by Kleinpell (1980). Although the Big Mountain microfauna reported by Cushman and LeRoy (1938) is relatively small, it contains *Marginulina dubia* Neugeboren, 1851, and *Nonion incisum kernensis* Kleinpell, 1938, which, by Kleinpell's (1980) criteria, are indicative of the upper part of the Zemorrian Stage (*Uvigerina sparsicostata* zone). Both of these taxa are restricted to this zone and no taxa of the Saucesian were reported from this area by Cushman and LeRoy (1938). Tipton *et al.* (1973) reaffirmed the interpretation of Cushman and Leroy (1938). In western Ventura County, a single specimen of a cricetid rodent (UCMP 96289) was found about 117 m (383 ft.) stratigraphically above the base of the Rincon Shale and within the reference section of the *Uvigerina sparsicostata* zone. Direct associations between continental fossil mammals and marine microfaunas are rarely reported but, unfortunately, this isolated specimen (UCMP 96289) is insufficient to provide a direct correlation between a North American Land Mammal Age and the "type" Zemorrian Stage. Marine–nonmarine faunal correlations in the Ventura Basin must be accomplished by less direct means at this time.

It may be recalled that Poore (1980) has a compelling argument for recognizing diachroneity for the Zemorrian–Saucesian boundary when the planktic foraminiferal zonation of the California Paleogene is used as a standard of reference. Blake (1983) has presented a bathymetric study based on benthic foraminifera from the Vaqueros Formation in the Big Mountain area and presented further suggestions for diachroneity of the Zemorrian–Saucesian boundary. According to Blake (1983), the lowest beds of the Vaqueros Formation in this area may be Zemorrian, whereas samples from higher in the section, and stratigraphically equivalent to the samples of Cushman and LeRoy (1938), positively indicate reference to the lower part of the Saucesian Stage. These data lend a caveat to the approximate date of 23 Ma for the Zemorrian–Saucesian boundary as determined by Turner (1970) because the common-stage boundary is apparently significantly diachronic and, therefore, in need of redefinition. The foraminiferal beds of the Vaqueros Formation in the vicinity of Big Mountain are interbedded with the "Vaqueros" Stage marine megafauna.

The Vaqueros Formation in the Big Mountain area has a stratigraphic thickness of approximately 447 m (1470 ft.). The lowest 91.5 m (300 ft.) is a massive sandstone that has produced an insubstantial sample of fossil marine invertebrates and rare marine and continental vertebrates. The diagnostic fossil taxa in this area have been collected from the middle and upper parts of the Vaqueros section. Although the upper 161 m (530 ft.) of the Vaqueros Formation is either upper Zemorrian or lower Saucesian and "Vaqueros" in age, the lowermost 195 to 286 m (640 to 940 ft.) have not yielded any foraminiferal data and cannot be confidently assigned to any of Addicott's (1972) revised marine molluscan stages. Kleinpell and Weaver (1963), however, have indirectly assigned this lower interval to the lower part of their "Vaqueros" Stage based on the presence of *Turritella inezana sespeensis* Arnold, 1907, and *Kewia fairbanksi* (Arnold, 1907). The upper Zemorrian is a correlative of the lower "Vaqueros" according to these authors. This problematic lower "Vaqueros" interval is not presently recognized at South Mountain, partly because published foraminiferal data for the Vaqueros Formation of South Mountain are lacking.

The age-diagnostic invertebrate fossils of the Big Mountain and South Mountain areas provide no more than a minimum age for the upper parts of the underlying Sespe Formation because the Vaqueros Formation rests unconformably on the Sespe Formation in both of these areas (Canter, 1974; Yeats, 1987). The Vaqueros Formation at South Mountain reaches a maximum thickness of 335 m (1100 ft.) (Baddley, 1954), and the marine megafauna that was reported by Loel and Corey (1932) was collected from the lowest 30 m.

Present interdisciplinary paleontologic correlations do not support the contention that the Alamos Canyon Local Fauna, from the uppermost beds of the Sespe Formation at Big Mountain, is overlain by foraminifera referable to the lower part of the Zemorrian Stage. The Zemorrian Stage is regionally tied to calcareous nannoplankton zones CP18 and

CP19 and possibly planktic foraminiferal zone ?P22 (McDougall, 1983). The succeeding Saucesian Stage has been recorded in association with nannoplankton referable to the upper part of zone CN1 (Newell *in* Lagoe, 1988). Other workers (Poore, 1980; Poore and Bukry, 1983) have reported microfossil associations that suggest the lower part of the Zemorrian Stage is correlative with zones CP18 and possibly CP19 as well as zones P19, P20, and possibly ?P21. According to Berggren *et al.* (1985), the minimum age of the early-late Zemorrian transition, if correlative with P21 and CP19, corresponds in age to the earliest Arikareean and can be no older than about 28 to 29 Ma. The Willard Canyon tuff date of 28.2 Ma, the overlying 264 m of Sespe Formation sediments, and the "Vaqueros" Stage fauna in the overlying Vaqueros Formation support the inference that the Vaqueros Formation at South Mountain is no older than late Zemorrian (*Uvigerina sparsicostata* chron). This interpretation is in agreement with the conclusions of Tipton *et al.* (1973) and, indirectly, with the Arikareean Age assignment of the South Mountain Local Fauna by Wilson (1949) and Schultz and Falkenbach (1949).

If the lower Zemorrian assignment given to the lower part of the Vaqueros Formation by Tipton *et al.* (1973) is accepted, then the fossil mammals from the subjacent Sespe Formation could not be younger than Orellan or possibly Whitneyan following the chronostratigraphic correlations of Berggren *et al.* (1985). The combined available chronostratigraphic data suggest that the early-late Zemorrian boundary is approximately coincident with the Orellan–Whitneyan boundary and precludes the possibility of an Arikareean "Age" for the Alamos Canyon Local Fauna. This discordance is resolvable either by recognizing the upper Sespe Alamos Canyon Local Fauna as Whitneyan (or older) or by recognizing the lowest beds of the Vaqueros Formation as upper Zemorrian or lower Saucesian, as Blake (1983) has suggested.

Wilson (1949) considered a Whitneyan North American Land Mammal Age assignment for the Alamos Canyon Local Fauna on the basis of the primitive stage of evolution of a single specimen, LACM (CIT) 3538, which he referred to *Archaeolagus* (Cope, 1881). Dawson (1958) reaffirmed his systematic conclusion. Although *Archaeolagus* first occurs in the Whitneyan of the Great Plains, Wilson (1949) refrained from assigning this fauna to the Whitneyan. A leptaucheniine that had been found approximately 305 m (1000 ft.) stratigraphically below the *Archaeolagus* specimen suggested to Wilson a correlation with the Arikareean "leptauchenid zone" of South Mountain and thereby precluded a Whitneyan Age for the Alamos Canyon Local Fauna.

Assignment of the fossil mammals from the upper 305 m (1000 ft.) of the Big Mountain–Alamos Canyon section of the Sespe Formation to the Whitneyan Age is consistent with present chronostratigraphic data. The age assignments of the mammalian and marine invertebrate fossils in the upper part of the Sespe Formation and the lower to middle Vaqueros Formation in this area are in accord following this rationale, but the lost leptaucheniine mentioned by Wilson (1949) would have to be recognized as older than the oreodonts of the "leptauchenid zone" of South Mountain. Because this specimen is presumed lost and not available for study, any further interpretation is conjectural. Alternatively, the recognition of the lowest beds of the Vaqueros Formation as late Zemorrian or early Saucesian provides further constraints, following Berggren *et al.* (1985) and McDougall (1983), that are in agreement with the mammalian and foraminiferal age assignments of Wilson (1949) and Blake (1983), respectively. In this case, the Alamos Canyon Local Fauna would more likely be Arikareean and correlative with the South Mountain Local Fauna.

## ARIKAREEAN-CENOZOIC EPOCH CORRELATION

Lander (1983) has contested some previous correlations of the early Arikareean with the latest Oligocene and early Miocene (Berggren *et al.*, 1978) and has proposed an early Arikareean NALMA–Refugian Pacific Coast benthic foraminiferal stage–late Eocene correlation. His interpretation is based on a suggested stratigraphic correlation between three fossil vertebrate specimens from the Sespe Formation in the Santa Ynez Mountains (western Transverse Ranges, Santa Barbara County) and Narizian ("Eocene") benthic foraminiferal faunas from the Sacate Formation. More defensible age estimates of Tertiary epoch boundaries and chronostratigraphic correlations are discussed in Berggren *et al.* (1985) and conflict with those proposed by Lander (1983).

The suggestion by Lander (1983:148) that the early Arikareean faunas from the Sespe Formation may be as old as 35 Ma conflicts with the isotopic age data from the Willard Canyon tuff. Because the isotopic ages for tuffs from the base of the Gering Formation (Table 2) are essentially identical to the age determination from the South Mountain Local Fauna (28.2), a 28 to 29 Ma age estimate is suggested for the early Arikareean NALMA. Isotopic age data from other Gering Formation correlatives (Tedford *et al.*, 1987) and the 32 to 36 Ma age data from volcanic rocks that are associated with Chadronian faunas in west Texas and Wyoming (reviewed by Wilson, 1986) are discordant with Lander's (1983) age estimate for the Arikareean.

Marine–nonmarine correlations in the Paleogene section of San Diego, California, supply further evidence for a post-Eocene age for the Arikareean NALMA (see May and Warme, 1987, for most recent review of San Diego "Eocene" stratigraphy). The Ardath Shale in the San Diego embayment has produced an early Uintan–late Bridgerian fauna

**Table 2. Compilation of the published age determinations for the lower part of the Gering Formation, northwestern Nebraska. Data from Obradovich *et al.* (1973) and Naeser *et al.* (1980).**

| Locality | Age (Ma) | Mineral | Method | Analyzer |
|---|---|---|---|---|
| Roundhouse Rock | 28.7 ± 0.7 | Biotite | $^{40}$K-$^{40}$Ar | Obradovich[1] |
| Helvas Canyon | 27.7 ± 0.7 | Biotite | $^{40}$K-$^{40}$Ar | Obradovich[1] |
| Helvas Canyon | 27.8 ± 3.1 | Zircon | Fission track | Not given[1] |
| Helvas Canyon | 27.6 ± 0.6 | Zircon | Fission track | Izett[2] |
| Helvas Canyon | 28.8 ± 0.8 | Zircon | Fission track | Naeser[2] |
| "Twin Sister's" | 27.7 ± 0.6 | Sanidine | $^{40}$K-$^{40}$Ar | Obradovich[1] |

[1] Obradovich *et al.,* 1973.

[2] Naeser *et al.,* 1980.

(Golz, 1976) as well as nannoplankton referable to CP12b (Bukry, 1980). If the marine Priabonian Stage of Europe is correlative with CP15 (Berggren *et al.,* 1985), then Lander's (1983) correlation of the Arikareean with the Eocene would inexplicably restrict the Uintan, Duchesnean, Chadronian, Orellan, and Whitneyan NALMAs within two nannoplankton zones (CP13 and CP14).

These data call into question Lander's (1983) lithologic and paleontologic correlations within the Santa Ynez Mountains. His conclusion that *Sespia* sp. from the Sespe Formation can be physically correlated with the marine invertebrate fauna from the Sacate Formation is suspect. Further studies in the structurally complex Santa Ynez Mountains are necessary to resolve the anomolous correlations presented by Lander (1983).

With respect to the "Unnamed local fauna" of Lander (1983) from the upper part of the Sespe Formation near Moorpark, Lander's (1983:143) "late Eocene? (Priabonian)" age assignment for this part of the Sespe is likewise not supported by the present evidence.

## SOUTH MOUNTAIN–GREAT PLAINS CONTINENTAL CORRELATION

Scattered fossil mammals from the upper part of the Sespe Formation at South Mountain (Table 3) include *Sespia californica* Stock, ?*Desmatochoerus thurstoni* (Stock, 1934), *Mesoreodon hesperus* (Stock, 1930) (following Schultz and Falkenbach, 1949, 1954, 1968), and geomyid rodents (Wilson, 1949). These taxa have affinities with the oreodonts and rodents that have been described from the Gering Formation of Nebraska and the Sharps Formation of South Dakota. The holotype of *S. californica* was found approximately 337 m (1100 ft.) below the Willard Canyon tuff and is, therefore, demonstrably older than 28.2 Ma. Ongoing studies of the stratigraphy and structure of the Sespe Formation in the South Mountain area may require modification of the stratigraphic interpretations presented in Figure 2 but the general stratigraphic relationships appear to be correct. The isotopic age determinations from the Gering Formation are discussed below.

*Sespia marianae* Schultz and Falkenbach, 1948, including the holotype from Wildcat Ridge of western Nebraska, was recovered from a level near the base of the Gering Formation and stratigraphically in association with dated tuffs. A number of K-Ar and fission track dates have been made on minerals from these tuffs. Obradovich *et al.* (1973) reported a $^{40}$K-$^{40}$Ar age on biotite from the Carter Canyon Ash in Helvas Canyon of 27.7 ± 0.7 Ma. The same ash yielded a fission track age on zircon of 27.8 ± 3.1 Ma. Naeser *et al.* (1980) reported additional fission track ages on zircon of 27.6 ± 0.6 Ma (analysis by Izett) and 28.8 ± 0.8 Ma (analysis by Naeser).

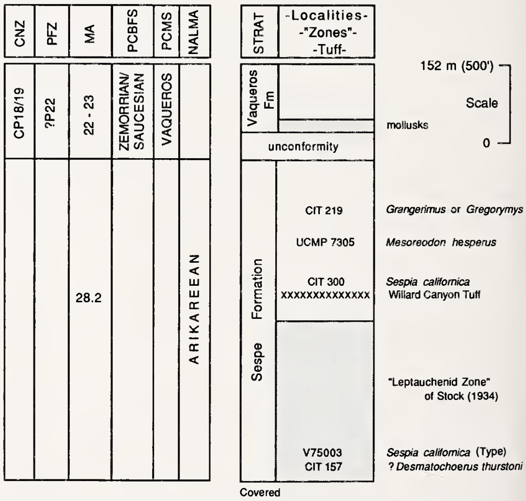

**Figure 2.** Generalized stratigraphic column and correlation chart for the Sespe Formation, South Mountain, California. Certain localities and taxa with less precise stratigraphic positions are not plotted; see faunal list (Table 3) for additional paleontologic and stratigraphic data. Abbreviations are as follows: NALMA, North American Land Mammal Age; PCMS, Pacific Coast Molluscan Stage; PCBFS; Pacific Coast Benthic Foraminiferal Stage; MA, megannum; PFZ, Planktic Foraminiferal Zone; CNZ, Calcareous Nannofossil Zone. Data from Stock (1930, 1934, unpublished), Wilson (1949), McDougall (1983), Poore and Bukry (1983), Yeats (1987), Turner (1970), and this paper.

A tuff from the lower part of the Gering Formation at Roundhouse Rock yielded a $^{40}$K-$^{40}$Ar age on biotite of 28.7 ± 0.7 Ma (Obradovich *et al.*, 1973). Although the tuffs from Roundhouse Rock and Helvas Canyon are from the lower part of the Gering Formation, it is not certain that they represent exposures of the same tuff, because outcrop exposures do not allow physical correlation of the two tuffs.

In addition to these dates, sanidine-bearing pumice from the middle part of the Gering Formation yielded a $^{40}$K-$^{40}$Ar age of 27.7 ± 0.6 Ma (Obradovich *et al.*, 1973). This pumice-bearing unit crops out stratigraphically above the dated tuffs at both Roundhouse Rock and Helvas Canyon and is known as the "Twin Sister's Pumice Conglomerate."

Tedford *et al.* (1987) list some of these ages for the calibration of the beginning of Arikareean time. A complete list of these data (Table 2) suggests a bimodal distribution, the ages being either approximately 28.7 or 27.7 Ma. The reason for the bimodal distribution of these ages was not given by these authors, and its explanation is not within the scope of this study. As a result, given the discrepancy in these age determinations, it is not possible to be certain whether the Willard Canyon tuff is older or younger than the basal part of the Gering Formation of Nebraska. If the tuffs at Roundhouse Rock and Helvas Canyon represent the same eruptive event, then the average of the biotite dates from these two localities and the average of the two better zircon dates from Helvas Canyon would be 28.2 ± 0.5 Ma, an age consistent with the age of the Willard Canyon tuff.

**Table 3. Fossil vertebrate faunal list by locality for the South Mountain Local Fauna, Ventura County, California.**

| | |
|---|---|
| Upper 305 m (1000 ft.) | |
| UCMP 7305 | ?*Mesoreodon hesperus* (Stock, 1930) |
| UCMP 7304 | Leptaucheniinae [lost?] |
| CIT 158 | Hypertragulidae |
| CIT 160 | Leptaucheniinae |
| CIT 167 | *Diceratherium* sp.<br>Leptaucheniiae |
| CIT 219 | *Grangerimus* sp. or *Gregorymys* sp. |
| ?CIT 166 | *Sespia* sp. |
| V82003 | Hypertragulidae |
| Approximately 200 to 335 m (650 to 1100 ft.) below top | |
| CIT 300 | *Sespia* cf. *S. californica* (Stock, 1930) |
| Approximately 335 to 640 m (1100 to 2100 ft.) below top "Leptauchenid Zone" of Stock | |
| CIT 157 | ?*Desmatochoerus thurstoni* (Stock, 1934)<br>*Sespia californica* (Stock, 1930)<br>*Sespia* sp.<br>Leptaucheniinae |
| CIT 159 | Leptaucheniinae |
| CIT 220 | ?*Mookomys bodei* Wilson, 1949 |
| V6101 | *Sespia californica* (Stock, 1930) |
| V6102 | *Sespia californica* (Stock, 1930) |
| V75003 | *Sespia californica* (Stock, 1930) |
| V67114 | Testudinidae |
| ?V2601 | *Sespia californica* (Stock, 1930) |

## CONCLUSIONS

The presence of the oreodont *Sespia californica* (Stock) and the 28.2 ± 0.2 Ma isotopic age determination associated with the South Mountain Local Fauna provide evidence for an "early" Arikareean Age for the fauna of the lowest exposed beds of the Sespe Formation at South Mountain (Fig. 2). The sparse fossil mammal sample known for the upper part of the Sespe Formation in this area is correlative in age to the fauna from the Gering Formation or possibly the fauna from the overlying Monroe Creek Formation—that is, either "early" or "middle" Arikareean. The age of the top of the Sespe Formation is constrained by the "Vaqueros" molluscan assemblage that has been recovered from the unconformably overlying Vaqueros Formation. The "Vaqueros" Age is correlative with the late Zemorrian and early Saucesian ages. Isotopic age determinations of 22 to 23 Ma are associated with the Zemorrian–Saucesian boundary and provide an estimate of the minimum age of the uppermost Sespe beds.

The Alamos Canyon Local Fauna, which includes all specimens from the upper 305 m (1000 ft.) of the Sespe Formation in the Big Mountain area, is suspected of being no older than Arikareean. Evidence for this interpretation is provided by the "Vaqueros" marine molluscan assemblage and the early Saucesian benthic foraminiferal assemblage that have been reported from the overlying Vaqueros Formation in this area.

The best fit of the combined evidence from the various geochronologic disciplines suggests an approximate age equivalence for the mammalian faunas of the uppermost beds of the Sespe Formation at South Mountain and Big Mountain, Ventura County, California.

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## ADDENDUM

Recent work by Howard (1989), published since the submission of this paper, provides additional field data pertaining to the correlation of the Refugian (marine) and the Arikareean (nonmarine) faunas proposed by Lander (1983). In the western Santa Ynez Range, Howard (1989) recognized a major unconformity in the nonmarine Sespe Formation a few meters below the fossil vertebrate locality (V5813) that was essential to Lander's Eocene age designation for the Arikareean North American Land Mammal Age. The lower part of the Sespe Formation, below the unconformity, grades laterally into the marine Gaviota Formation of Refugian (late Eocene) age (Howard, 1989). Stratigraphically above the unconformity, the upper part of the Sespe contains the Arikareean (late Oligocene) fauna and grades laterally into the sparsely fossiliferous Alegria Formation (or Alegria member of the Vaqueros Formation following Rigsby [1988]). The duration of the unconformity is suggested by the lack of latest Eocene through mid-Oligocene (Chadronian-Whitneyan) nonmarine fossils in the upper Sespe section. The unconformity is attributed by Howard (1989) to global drop in sea level at 31 Ma. This new data corroborates our conclusions proposed here, based on radioisotopic and paleontologic data, that the Arikareean faunas of the upper part of the Sespe Formation are late Oligocene in age.

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# A NEW GENUS AND SPECIES OF PLETHODONTID SALAMANDER FROM CHIAPAS, MEXICO

DAVID B. WAKE[1] AND JERRY D. JOHNSON[2]

**ABSTRACT.** A new species of plethodontid salamander from the mountains of northern Chiapas, Mexico, is so distinct from all described species that it is placed in a new genus. This taxon, *Ixalotriton niger,* is known only from a small patch of cloud forest near Berriozábal, Chiapas. This slender, active, scansorial species has very long arms, legs, and digits, and it has broadly expanded terminal phalanges that have hook-like processes. The tail is long and slender. All specimens are nearly uniformly black. The only species that resembles the new species in morphology is *Nyctanolis pernix,* another long-legged, slender, scansorial form from nuclear Central America. However, *Nyctanolis* differs from all other tropical genera, including *Ixalotriton,* in having divided premaxillary bones, an ancestral trait. In most osteological characters *Ixalotriton* resembles members of *Pseudoeurycea,* a group thought to be paraphyletic. The habitat of the new genus is rapidly disappearing and immediate conservation measures are required if this novel species is to survive.

**RESUMEN.** Una nueva especie de salamandra plethodóntida de las montañas del norte de Chiapas, México, es tan diferente de todas las descritas que se la coloca en un nuevo género. Este taxon, *Ixalotriton niger,* se conoce solamente de una pequeña área de bosque nublado cerca de Berriozábal, Chiapas. Esta especie es elongada, activa y trepadora, posee miembros anteriores y posteriores y dígitos largos, y falanges terminales ensanchadas con procesos en forma de gancho. La cola es larga y fina. Todos los ejemplares son casi uniformemente negros. La única especie que se le asemeja en morfología es *Nyctanolis pernix,* otra salamandra elongada de patas largas y trepadora de América Central. Sin embargo, *Nyctanolis,* a diferencia de todos los demás géneros tropicales, incluyendo *Ixalotriton,* posee huesos premaxilares divididos, un rasgo ancestral. En la mayoría de los caracteres osteológicos *Ixalotriton* se parece a *Pseudoeurycea,* un grupo considerado parafilético. El habitat de este nuevo género está desapareciendo rapidamente, y se requieren medidas de conservación inmediatas para que esta nueva especie sobreviva.

## INTRODUCTION

In January, 1973, J.D. Johnson collected a series of highly active, arboreal salamanders in a humid forest in northwestern Chiapas, Mexico. Subsequent visits to this area have resulted in additional specimens, but despite a substantial amount of fieldwork the species has not been found elsewhere. Upon examining preserved specimens in 1973, D.B. Wake recognized that they represented a distinct species. During the intervening years we have sought to determine the most appropriate genus in which to place this species. Wake and Lynch (1976, Appendix) referred this undescribed species to *Chiropterotriton* beta. Subsequently, the beta species group was divided and the species were assigned to two new genera (*Dendrotriton* and *Nototriton* Wake and Elias, 1983), and the new species did not fit well into either of them. At a later date a superficially similar species was discovered in Chiapas and adjacent Guatemala, and for a time we thought that these two species formed a natural group. However, detailed anatomical study revealed that the second species (placed in a new genus, *Nyctanolis* Elias and Wake, 1983) differed from all tropical salamanders in having paired premaxillary bones, a character considered to be of significant cladistic importance (Wake, 1966; Wake and Larson, 1987). At this point it became evident that among currently recognized genera only *Pseudoeurycea* could possibly accommodate this new taxon. However, *Pseudoeurycea* contains a diverse group of species and is suspected to be paraphyletic (Wake and Elias, 1983). To add this unique new taxon to such a heterogeneous conglomerate would be both inappropriate and uninformative. The new taxon and *Pseudoeurycea* share no unique synapomorphies.

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[1] Department of Zoology and Museum of Vertebrate Zoology, University of California, Berkeley, California 94720; Research Associate in Herpetology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

[2] Department of Biology, El Paso Community College, El Paso, Texas 79998, and Department of Biological Sciences, University of Texas at El Paso, El Paso, Texas 79968.

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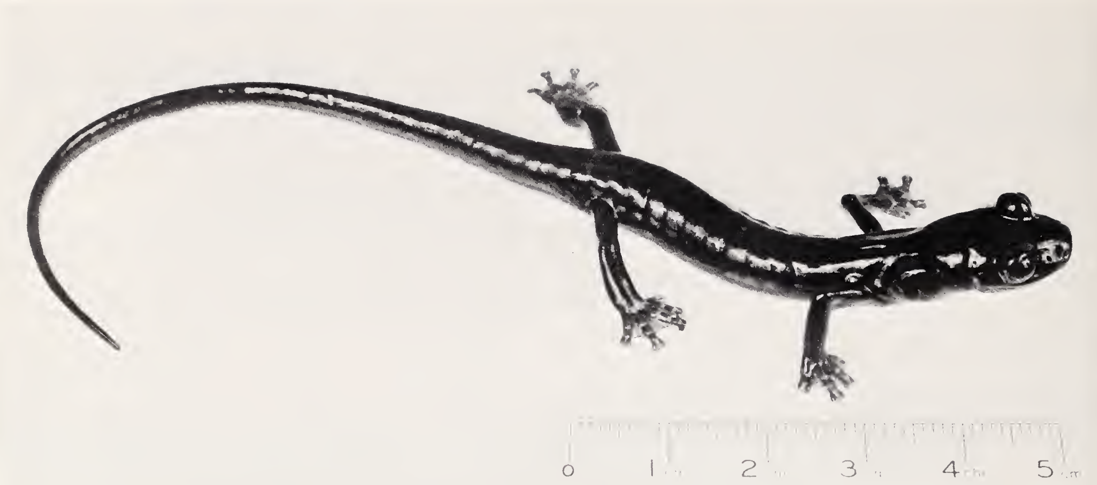

**Figure 1.** Photograph of a live *Ixalotriton niger* new genus, new species, MVZ 158822, collected at the type-locality. This individual has a parasite-induced tumor on the side of the neck.

Accordingly, we have chosen to place this unique new species in a new genus.

## *Ixalotriton* new genus

**TYPE-SPECIES.** *Ixalotriton niger* new species.

**DIAGNOSIS.** A genus of plethodontid salamanders belonging to the subfamily Plethodontinae, tribe Bolitoglossini, supergenus *Bolitoglossa*. Members of *Ixalotriton* are relatively large, with long legs, fingers, toes, and tails. The genus differs from the only similar taxon, the stouter *Nyctanolis*, in having a single premaxillary bone and in lacking any dorsal markings on its solid black ground color. No other tropical salamanders have such long legs or large hands and feet (when adpressed to the body the legs overlap for 2 to more than 4 costal interspaces). In addition, *Ixalotriton* differs from *Chiropterotriton* in lacking septomaxillary bones and having a fifth metatarsal smaller than the fourth, and from *Bolitoglossa* in having a sublingual fold. *Ixalotriton* is most similar to *Pseudoeurycea* in osteology but differs from all members of that genus in having very long limbs, digits, and tail. The new genus differs from all other members of the supergenus *Bolitoglossa* by the combination of its large size, generalized osteological structure, and long limbs, digits, and tail.

**ETYMOLOGY.** From *ixalos*, Greek, meaning bounding or springing, in reference to its behavior; and *triton*, Greek, a commonly used term for salamanders. The gender is masculine.

## *Ixalotriton niger* new species

Figures 1–4

**HOLOTYPE.** Museum of Vertebrate Zoology (MVZ) 158823, an adult female from 12 km (7.5 mi) NW Berriozábal, Chiapas, Mexico, elevation ca. 1,068 m, collected on December 26, 1980, by Jerry D. Johnson.

**PARATYPES.** MVZ 143837–38, 158822, 160952–58, 160960–63, 184891–92 (cleared and stained); Natural History Museum of Los Angeles County (LACM) 137512; Laboratory for Environmental Biology, University of Texas at El Paso (UTEP) 5796–98; same locality data as holotype, collected on different dates.

**DIAGNOSIS (measurements in millimeters).** See Generic Diagnosis. A large, slender species (standard length, SL, of ten adult males 53.2–59.7, mean 56.6; nine adult females 51.1–58.9, mean 54.4) with a long, strongly tapered, slender tail (SL/tail length of six adult males 0.64–0.74, mean 0.68; seven adult females 0.7–0.88, mean 0.76) and long limbs and digits (when adpressed to the sides of the trunk the fore and hind limbs overlap for 2.5 to more than 4, mean 3.7, costal grooves in ten adult males, and 2 to 4, mean 3, in nine adult females). The head is broad and flat (SL/head width of ten adult males 5.8–6.2, mean 6.0; nine adult females 5.9–6.8, mean 6.4). There are large numbers of very small premaxillary–maxillary (ten adult males have left plus right totals of 78–150, mean 120; nine adult females have 110–143, mean 125) and vomerine (ten adult males have left plus right totals of 31–47, mean 40; nine adult females have 37–52, mean 42) teeth. Coloration of the species is distinctive—all specimens are a solid, glossy black by day (becoming brown by night), with a little white pigment in the snout region and red-tinted (probably from the dense capillary beds) toe tips.

**DESCRIPTION.** This is a moderately large, slender species with a broad, depressed head and large, strongly protuberant, prominent eyes (Fig. 1). The snout is rather long and broad, and is strongly flattened. The nostrils and white-tipped nasolabial protuberances are small in both sexes, but more broad-

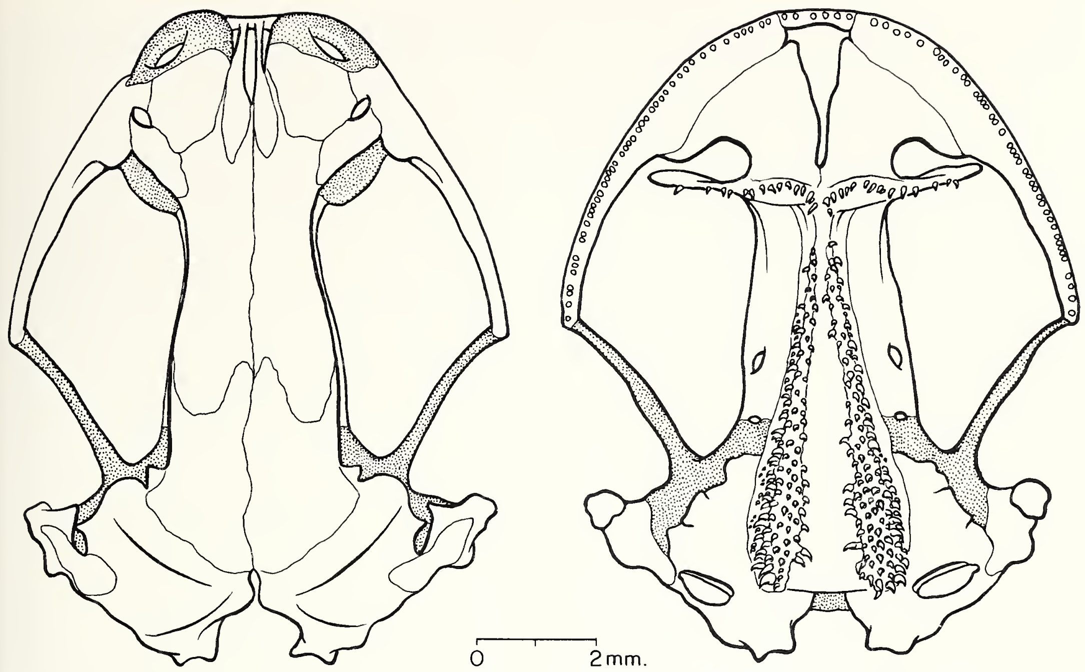

**Figure 2.** Dorsal and ventral views of the skull of *Ixalotriton niger* new genus new species, MVZ 184892. Cartilage is stippled.

ly based and pronounced in the males. Snouts of both sexes are similar, and there is only a moderate extension anteriorly beyond the tip of the lower jaw. All males have a round mental gland that, while prominent, never has a diameter more than about one-third the width of the head. The broad, flattened head is much broader than any other part of the body. The ratio of maximum head width to head depth at the angle of the jaw generally exceeds 3. An unpigmented groove extends below the anterior and middle parts of the eye, following its curvature, but this groove does not communicate with the lip. The large eyes stand out prominently above the head, but they extend only slightly, if at all, beyond its lateral margins. A weakly defined postorbital groove extends posteriorly from behind the eye as a shallow depression which meets the upper end of the nuchal groove. The nuchal groove proceeds ventrally at the angle of the lower jaw and proceeds across the gular region, at first as a well-marked groove and then as an indistinct slight depression. The small vomerine teeth are arranged in a long series that is a flattened curve lying almost perpendicular to the midline. The series curves slightly posteriorly at the lateral end, and there is a sharp bend near the midline where the series ends by becoming directed toward the posterior vomerine tooth patch. The tooth series extends well beyond the lateral margin of the internal naris. Medially the two series do not come into contact, and there is a small gap between the posteromedial end of the series and the posterior patch. The patch is similar to that which occurs in other members of the supergenus *Bolitoglossa,* being shaped like an inverted teardrop. It is bilaterally symmetrical and each half contains in excess of 75 tiny teeth. The result is a large shagreen-like surface on the roof of the mouth that extends posteriorly, beyond the glottis, into a kind of pouch. Maxillary and premaxillary teeth are numerous. The maxillary teeth extend posteriorly in a long series that ends at approximately the level of the posterior margin of the opening for the eye. The maxillary and premaxillary teeth are similar in size and morphology, and there is no evident break in the series on adjacent bones. Both premaxillary and maxillary teeth are small. The premaxillary teeth are relatively few—six in each of the cleared and stained animals. The premaxillary teeth of males are usually not differentiated from maxillary teeth, or from premaxillary teeth of females; but in some of the males, including one of the cleared and stained animals, the premaxillary teeth can be large. In the cleared and stained animal there are six teeth on the premaxillary bone and three of them are large. The middle tooth is exceptionally long, over five times the length of the typical crown, and it is monocuspid, with the labial cusp apparently absent. The tongue pad is nearly round and lies at the end of a distinct pedicel. There is no anterior attachment, and the tongue has the boletoid form characteristic of the supergenus *Bolitoglossa.* A large, fleshy sublingual fold is present.

The trunk and tail of this species are slender and cylindrical. There is a distinctly shortened segment at the base of the tail, which is slightly constricted at this point, but the tail can also be autotomized distally. The tails are very long, slender, and strongly tapered, becoming very narrow and whip-like near the tip. The postiliac spot is distinct in some individuals and indistinct in others. The limbs are extremely long. The hands and feet are large, with long digits. The limb segments are exceptionally long and slender. There is a moderate amount of webbing at the base of the digits. The webbing extends to the level of about the middle of the first phalanx of the longest digit of both hands and feet. All but the first digit of both hands and feet have broadly expanded, flattened tips. The fingers are, in order of decreasing length, 3,4,2,1; the toes, 3,4,2–5,1.

**MEASUREMENTS OF THE HOLOTYPE (in millimeters).** Head width 8.6; snout to gular fold (head length) 13.2; head depth at posterior angle of jaw 3.5; eyelid length 3.8; eyelid width 2.0; anterior rim of orbit to snout 3.3; horizontal orbit diameter 3.4; interorbital distance 2.7; distance between vomerine teeth and parasphenoid tooth patch 0.5; snout to forelimb 16.8; distance separating internal nares 3.0; distance separating external nares 3.0; snout projection beyond mandible 0.8; snout to posterior angle of vent (SL) 58.2; snout to anterior angle of vent 53.8; axilla to groin 31.0; tail length 81.6; tail width at base 3.2; tail depth at base 3.8; forelimb length (to tip of longest toe) 18.2; hindlimb length 19.2; width of right hand (across digits, from tip of innermost to tip of outermost digits) 5.1; width of right foot 7.5.

**COLORATION.** In life (by day) the animals have a glossy black color that is very dark dorsally, and the venter is a lighter, dark gray color. The ground color lightens to a brown appearance at night. The nasolabial protuberances are inconspicuously lightened, due to a reduction in melanic concentration. The dark iris has some golden-brown highlights. The toe tips appear reddish, evidently due to the low concentration of melanin and the presence of extensive vascularization. In alcohol the black coloration has lightened to varying degrees, but the contrast between the darker dorsum and the somewhat lighter venter persists. There are two relatively depigmented areas, which appear as lightened patches, near the front of the head, and these are more prominent in males than in females. The hands and feet also are very dark in color, although a bit lighter than the middorsal part of the trunk.

**OSTEOLOGY.** Information has been derived from two cleared and stained specimens (MVZ 184891–92, a male and a female, respectively) and from radiographs of the type-series. Dorsal and ventral views of the skull are illustrated (Fig. 2).

The skull is exceptionally broad and flattened, and the anterior cranial elements are not tightly articulated; the skull appears to be rather loosely organized anterior to the eyes. The bones are all well defined, but several of them are thin. The single premaxillary bone bears a rather narrow dental process and is relatively small, especially in comparison with the paired premaxillary bones found in *Nyctanolis*. The premaxillary is either loosely articulated, or makes no contact at all, with the maxillary bones. The premaxillary has no palatal process. Frontal processes of the premaxillary are slender and they arise near each other, but separately. The internasal fontanelle is small and narrow. Near the dorsal surface of the skull the premaxillary frontal processes become flattened and somewhat expanded, and the expanded portions may come into contact on the midline. The expanded portions extensively overlap the facial region of the frontal bones, but they have no or extremely limited contact with the nasals. The frontal processes terminate rather far posteriorly, behind the nasals and at the level of, or even posterior to, the bony rim of the orbits. The moderately large nasals are protuberant in males, in which an anteromedial lobe extends forward beyond the premaxillary and dentaries to be the anteriormost part of the skull. In females the nonprotuberant nasals are rather quadrangular in shape. The nasals have almost no articulations with other bones but are flattened, scale-like elements that lie on top of the cartilaginous nasal capsules. There is a weak articulation with the facial portion of the frontal, and the anterolateral lobe is slightly overlapped by the facial lobe of the maxillary. No septomaxillaries have been found. Prefrontal bones are relatively well developed. These rectangular elements are between one-third and one-half the size of the nasals, and they have extensive articulation with the frontals and the facial lobes of the maxillaries. They may make a slight contact with the nasals. The nasolacrimal duct passes between the front end of the prefrontal, the lateral lobe of the nasal, and the facial lobe of the maxillary. The facial lobe of the maxillary is normally incised to provide space for the duct, and the anterior face of the prefrontal is normally concave, and may be incised, to accommodate the duct. The duct passes over the dorsal surface of the prefrontal, which is somewhat depressed and grooved anterolaterally. The maxillary bones are large and well developed, with relatively well-developed facial lobes and palatal shelves. The bones are well articulated to both the prefrontals and the vomers. The dental portion of the maxillary extends almost to the posterior limit of the eye, where it terminates in a relatively sharp point. The maxillaries bear a long series of small, bicuspid teeth.

The vomers are large and well developed. The intervomerine fontanelle is relatively small and is abruptly pinched off posteriorly, where the two vomers are well articulated to each other. The preorbital processes of the vomers are long and well developed, but relatively slender. They extend beyond the lateral margins of the vomer bodies and bear teeth in a long, relatively straight row to about the level of the lateral border of the bony opening for the nares (but well lateral to the internal nares themselves). The vomerine teeth are of about the same size as the maxillary teeth.

Frontals and parietals are broad, well-developed bones that are firmly articulated with each other in a complex, interlocking network, with large lateral lobes of the frontals overlapping the parietals and small medial lobes of the parietals overlapping the frontals. The paired frontals and the paired parietals are tightly articulated to each other along the midline, and here, too, the articulation involves interlocking portions of the elements. The facial portion of each frontal is relatively large and contributes importantly to the anterior part of the skull. The parietal is a simple bone but it does have a slight ventrolateral tab, characteristic of the supergenus, overlying the cartilaginous portion of the braincase immediately posterior to the orbitosphenoid. The interorbital region of the skull is rather broad, although it is somewhat narrower anteriorly than posteriorly.

The parasphenoid is large and relatively broad anteriorly, with a blunt anterior tip. The orbitosphenoids are rather vertical in orientation, although tipped medioventrally. Posterior vomerine teeth are borne in long, relatively narrow patches that become increasingly well separated from each other posteriorly. The teeth in these patches are somewhat smaller than the maxillary teeth. In the two cleared and stained specimens there are totals of 154 and 192 teeth in the two patches. The otic capsules are large and well developed, and there are distinct rounded ridges which mark the paths of the enclosed semicircular canals. There are no crests, but there is a small spur directed laterally, over the anterodorsal process of the squamosal. The operculum has a short, but distinct, columnar stilus. The stout, well-developed quadrates are connected to the otic capsules by broad squamosals and by the cartilaginous suspensorium. The squamosals are broad dorsally, with a distinct anterior process. Posterodorsally the squamosal bears a large, lobed process that lies over the posterolateral part of the otic capsule.

The lower jaw has a long, slender dentary that bears a very long series of small teeth, similar in size to those on the maxillary. There are 67–72 and 59–61 dentary teeth in the two cleared and stained animals. The prearticular is well developed and has a coronoid process that is bent mediodorsally.

The hyobranchial apparatus is relatively generalized in structure for a member of the supergenus *Bolitoglossa* (Fig. 3). The apparatus is entirely cartilaginous. There is no urohyal. The basibranchial bears relatively short radii that are continuous with it, and there is a small but distinct and partially discontinous lingual cartilage. The epibranchials are long, approximately 3 times the length of the basibranchial. The first ceratobranchials are extremely slender, whereas the second ceratobranchials are relatively stout. The long ceratohyals have a generalized form, with no anterior extensions or medial processes. The blade is relatively broad and flattened, with a bluntly sharp anterior terminus.

The vertebrae have a generalized structure with no especially distinctive features. Spindle-shaped intervertebral cartilages join the adjacent vertebrae, which appear to have bony husks that are tapered toward the center and thus appear amphicoelous. There is a single atlas, 14 trunk, one sacral, two caudosacral, and a variable number of caudal vertebrae. The atlas bears a pair of posterolaterally directed processes on the ventrolateral margins of the centrum, but there are no other ventral processes of note. A low dorsal crest is present on the neural arch of the first three to four trunk vertebrae. Transverse processes on the trunk vertebrae arise and remain separated for their entire length, and the rib heads also are separate structures. Ribs are borne on all trunk vertebrae but the last, and only the first and last pairs of ribs are noticeably shortened relative to the remainder. While ribs are relatively long, a rib on a mid-trunk vertebrae is slightly shorter than the distance across the transverse processes, and that distance in turn is slightly less than the length of the centrum. Spinal nerve routes are like those of other members of the supergenus *Bolitoglossa* (Elias and Wake, 1983).

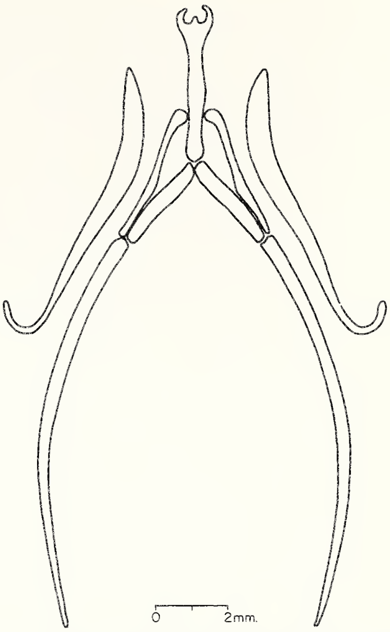

**Figure 3.** Dorsal view of the hyobranchial apparatus (totally cartilaginous) of *Ixalotriton niger* new genus, new species, MVZ 184892. The ceratohyals have been moved laterally for purposes of illustration.

The first caudosacral vertebra has transverse processes that are relatively long and straight and are oriented mainly laterally and a little posteriorly. The processes of the second caudosacral vertebra are considerably shorter, and they usually make a distinct posterior bend about mid-way along their length. These processes are always substantially shorter than those of the first vertebra. These processes arise fairly far anteriorly on the second cau-

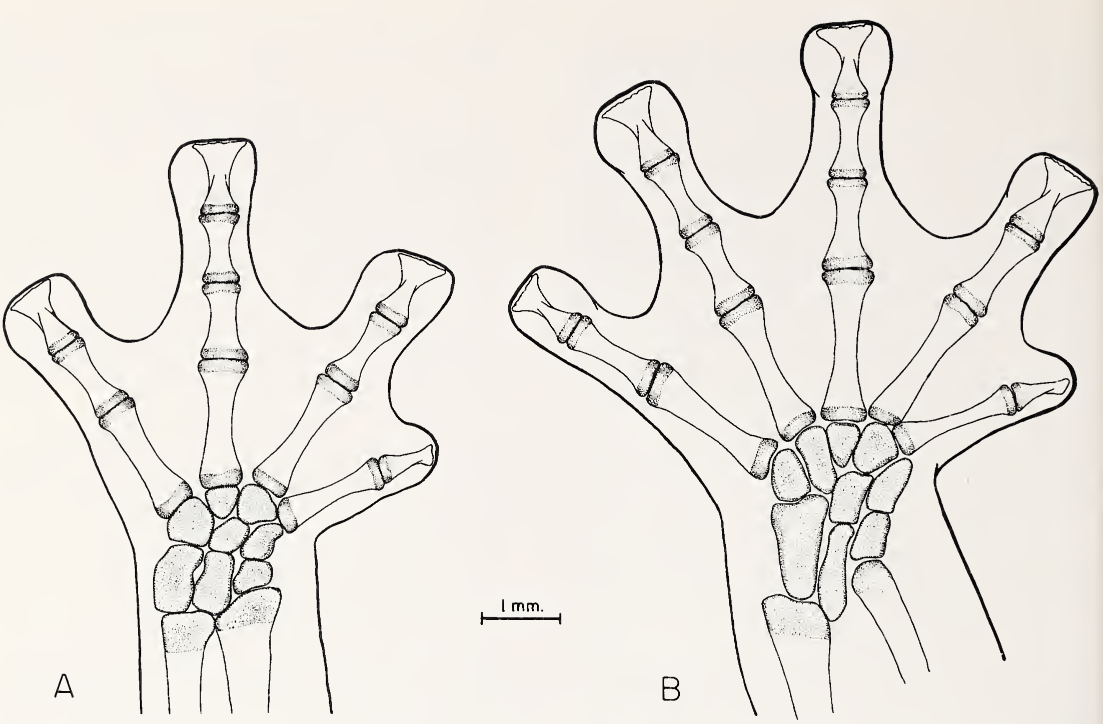

**Figure 4.** Dorsal view of the right hand (**A**) and right foot (**B**) of *Ixalotriton niger* new genus, new species, MVZ 184891. Cartilage is stippled.

dosacral vertebra, in front of the midpoint. The second caudosacral vertebra is the first to bear a complete haemal arch, but it lacks a haemal spine. The transverse processes of the first caudal vertebra are long and slender and are oriented sharply anterolaterally, arising from the extreme anterior end of the vertebra. They extend forward approximately to the level of the midpoint of the second caudosacral vertebra, but they do not overlap the processes of that vertebra. Transverse processes of succeeding vertebrae are located in the far anterior position, and they become progressively short posteriorly. However, they are readily apparent at least until the twentieth vertebra.

Individual caudal vertebrae are long and slender. Complete tails are rare, but in the cleared and stained specimen with a complete tail there are 48 vertebrae. There is a slight change in length at vertebra 37 which suggests that even in this animal there might have been loss of the tail tip early in life. Other animals that appear to have complete tails have between 48 and 52 trunk vertebrae.

The exceptionally long limbs contain individual bones that are long and slender. They are simple elements with no special processes. No tibial spur has been seen, although there is a low ridge in the area where it is normally found. The large hands and feet bear long digits made up of well-developed metacarpals, metatarsals, and phalanges (Fig. 4). The phalangeal formula is 1,2,3,2 for the hand and 1,2,3,3,2 for the foot. The very long metapodial elements and all but the terminal phalanges are simple cylindrical bones. The three longest fingers and the four longest toes have terminal phalanges that are highly specialized in structure. These elements are strongly flattened and expanded distally, so that they are more than twice the basal diameter of the phalanx. The expanded portion is bent downward, so as to form a cup-like depression on its underside. The outer margin of the phalanx extends into the skin and is serrated. On the underside of each terminal phalanx, just a little distal from the bony proximal end of the element, is a low knob, which serves as the point of insertion of the digital tendon and provides a mechanical advantage in bending the toe tip.

The carpal and tarsal arrangements are those characteristic of primitive plethodontids and are found in various other members of the supergenus *Bolitoglossa*, such as *Pseudoeurycea* (Wake and Elias, 1983, fig. 7A). There are eight carpals and nine tarsals. Distal tarsal 5 is smaller than distal tarsal 4, and it does not articulate with the centrale.

**KARYOTYPE.** James Kezer examined the chromosomes of one male and has kindly provided the following information and photograph. The haploid chromosome number is 13, as in all other members of the supergenus *Bolitoglossa* (Fig. 5). There is no male heteromorphism of the kind that has been found in *Oedipina*, *Nototriton*, *Dendrotriton*, and *Thorius* (Leon and Kezer, 1978; S.K. Sessions, pers. comm.). The particular individual examined had a reciprocal translocation, which is rare in salamanders. The ring of four chromosomes formed

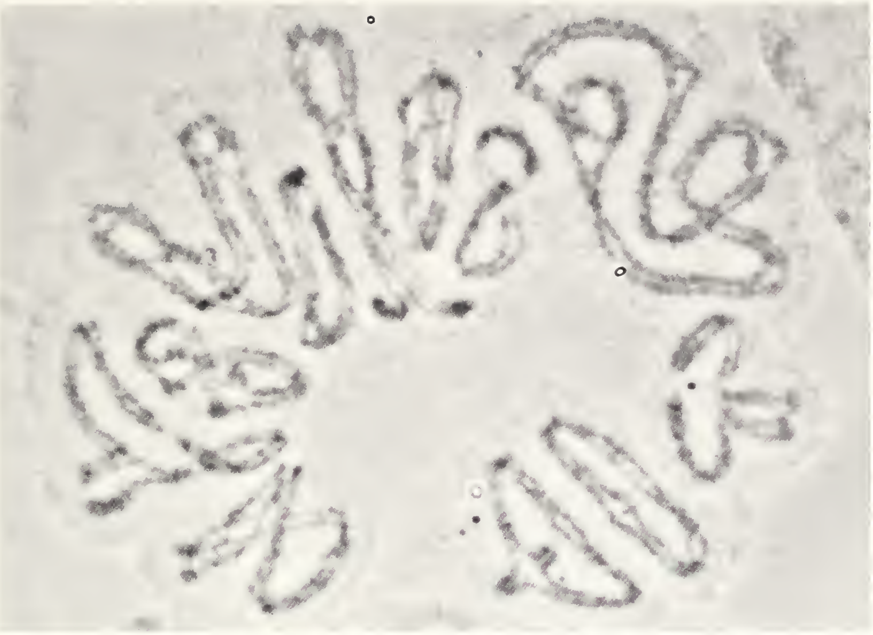

**Figure 5.** Karyotype of *Ixalotriton niger* new genus, new species, prepared and photographed by James Kezer. N = 13. Note that this individual has a reciprocal translocation, and this diplotene spread has a ring of four chromosomes.

at diakinesis (Fig. 5) includes a deeply interstitial chiasma, which is frequently present in bolitoglossines. Because only one individual has been examined, it is not known if this phenomenon is characteristic of the species.

**HABITAT AND BEHAVIOR.** *Ixalotriton niger* inhabits a moist evergreen forest at about 1,100 m elevation on the Caribbean versant of the Northern Highlands physiographic region of Chiapas, Mexico (described by Müllerried, 1957, and Breedlove, 1973). The area where salamanders were collected surrounds an abandoned oil well (Pozo Turipache) and is locally known as "Linda Vista." The locality is approximately 3 km NW of "El Suspiro," an abandoned coffee finca. Coffee is cultivated extensively in the area, and that activity has resulted in the cutting of much of the native forest vegetation. The locality is part of the southernmost ridge of the Northern Highlands that extends from Sumidero Canyon, north of Tuxtla Gutiérrez, Chiapas, westward to southeastern Oaxaca. Clouds gather consistently along this ridge as moist air flows from the Gulf of Mexico, located approximately 180 km to the north. Clouds usually cover the area beginning in mid- to late afternoon and lasting through early morning hours. During the dry season, clouds are sometimes absent. Rainfall data are not available for the type-locality, but records from Villahermosa, Tabasco, and Palenque, Chiapas, which are also located on the Caribbean versant, indicate a seasonal pattern of rainfall with a rainy season from early summer through late fall (Wernstedt, 1972). In the region of the type-locality, winter rains usually are associated with frontal systems ("nortes"), which periodically sweep in from the north. Even during the winter dry season sufficient precipitation falls to maintain moist conditions in the leaf litter on the forest floor, and in some years rainfall may be heavy. We estimate that rainfall averages around 3,000 mm per year. Temperatures at night reach as low as 14 C at night and as high as 32 C during the day. Average temperatures range from 17 C at night to 23 C during the day. The lowest temperatures occur during winter "nortes" and the highest temperatures are recorded during spring periods of the dry season (April and May).

The substratum located in the area is composed of rough, jagged limestone containing many sinks and crevices. The karst topography results in almost total absence of surface water.

Vegetation at the type-locality is montane rainforest, as classified by Breedlove (1973). The forest physiognomy is composed of two canopies of straight-trunked, large to medium-sized trees, with an understory of broad-leaved forbs and ferns. The larger trees usually have great burdens of epiphytic plants such as philodendrons, bromeliads, and orchids, which are more numerous on branches higher in the canopy. Most tree trunks and limbs are covered with a growth of mosses, sometimes in conjunction with small ferns and vascular plants, and fungi. The understory plants have become more abundant in recent years, probably due to the effects of cutting large trees, which allows more sunlight to penetrate to the forest floor.

The microhabitat requirements and behavior of *Ixalotriton niger* are mostly unknown. All specimens were collected during the winter months of

December and January, when "nortes" produced precipitation or heavy cloud cover. Extensive searches during summer months revealed no salamanders of this species. Most individuals, including the holotype, were found on the trunks of large and medium-sized trees, although a few were on leaves of understory forbs, and two individuals were found crawling on limestone boulders. All individuals were collected at night. It is unknown if the salamanders spend daytime hours in the cracks and holes of the limestone substratum or if they descend at night from moist habitats in canopy epiphytes (*e.g.,* bromeliads). The former is supported by the number of individuals found on lower vegetation and on the limestone boulders. In addition, Dennis E. Breedlove (pers. comm.) has found no salamanders in epiphytes during field investigations of vegetation of the area.

The escape behavior observed during capture of *Ixalotriton niger* primarily consisted of leaping away from a tree trunk or off of an understory leaf. The jumping action is similar to that of *Anolis.* The tail appears to be used as a spring. In the laboratory the animals had quick movements, relative to most salamanders, and they were observed to leap from one end of a container to the other. As is common in tropical plethodontids, the tail autotomizes near the base, but perhaps more readily than in most species. During capture some salamanders lost distal segments of the tail. When captured by hand, salamanders secreted a noxious-smelling, sticky substance. Charles A. Ely developed a skin rash after handling a specimen, possibly an effect of the secretion.

The only other commonly observed members of the herpetofaunal community at the type-locality were a frog (*Eleutherodactylus stuarti*) and a lizard (*Anolis parvicirculata*). When *Ixalotriton niger* was active, it was more abundant than these species. The number of salamanders, observed on recent visits, was low, likely a result of continued cutting of natural vegetation. The following species of amphibians and reptiles have been collected from the vicinity of the type-locality: salamanders—*Bolitoglossa mexicana, B. occidentalis*; frogs—*Agalychnis moreleti, Anotheca spinosa, Eleutherodactylus rhodopis, E. stuarti, Smilisca baudinii, S. cyanosticta,* and an undescribed species of leptodactylid frog; lizards—*Anolis laeviventris, A. parvicirculata, A. petersi, Celestus rozellae, Laemanctus longipes, Lepidophyma flavimaculatum, Sceloporus internasalis, S. variabilis, Sphenomorphus assatus, Xenosaurus grandis*; snakes—*Imantodes cenchoa, Lampropeltis triangulum, Leptodeira septentrionalis, Leptophis mexicanus, Micrurus elegans, Ninia diademata, N. sebai, Pliocercus elapoides, Pseustes poecilonotus, Rhadinaea decorata, Stenorrhina degenhardtii.* Johnson *et al.* (1977) discussed some of the species occurring at this locality.

Amphibians and reptiles that are most likely to share microhabitat with *Ixalotriton niger* include the species of *Bolitoglossa* and *Eleutherodactylus* listed above, as well as *Anolis parvicirculata, A. laeviventris, Celestus rozellae, Sphenomorphus assatus,* and *Xenosaurus grandis.* In addition, *Imantodes cenchoa* often was encountered while we were searching for salamanders in low vegetation and on limestone boulders, and it may prey upon the species.

*Ixalotriton niger* may be endangered, especially if it is a localized species that occurs only in the vicinity of the type-locality, where the forest is rapidly being cut for agricultural purposes and lumber. We predict that the natural forest in this area will be completely destroyed within the next few years, if this has not already occurred. Removal of the forest likely will result in the extinction of *I. niger,* which apparently has both a restricted geographic range and narrow habitat and microhabitat tolerances.

**RANGE.** The species is known only from the immediate vicinity of the type-locality in northwestern Chiapas, Mexico.

**ETYMOLOGY.** The name *niger,* Latin, is chosen because of the uniformly dark blackish color of the species.

## DISCUSSION

The relationships of *Ixalotriton* are obscure, and we have withheld publication of this taxon for some time while we have attempted to obtain specimens for biochemical studies and have searched for additional populations. *Ixalotriton* is clearly a member of the supergenus *Bolitoglossa,* for it possesses all of the critically important features of the tongue that characterize that group (Lombard and Wake, 1977), as well as the synapomorphic karyotype, with a haploid chromosome number of 13 (Leon and Kezer, 1978; Elias and Wake, 1983). However, the relationships of *Ixalotriton* within that supergenus are less clear.

Wake and Elias (1983) listed 18 potentially useful characters for cladistic analysis of the tropical plethodontid genera. Of these characters, seven are apparently autapomorphies that are useful only in defining monotypic genera but are not otherwise informative. One of these characters, the presence of unusually long limbs, is shared with *Nyctanolis* and is a potential synapomorphy for these two genera. The remaining 11 are synapomorphies for two or more genera. *Ixalotriton* has three of these derived traits: no tibial spur (shared with *Dendrotriton* and *Oedipina*), no septomaxillary bones (shared with *Bolitoglossa, Bradytriton, Lineatriton, Nototriton, Nyctanolis, Parvimolge, Oedipina,* and *Thorius*), and a single premaxillary bone (shared with all but *Nyctanolis*). The only one of these characters that appears to be informative is the presence of a single premaxillary bone, which serves to link it cladistically to all genera except *Nyctanolis,* the one genus it resembles most closely in overall structure and habits. In fact, one of its other potential synapomorphies is the only derived trait previously listed for *Nyctanolis,* very long legs.

The two remaining traits are not very useful for they are known to vary within genera. Derived conditions were coded by Wake and Elias (1983) on the basis of presence in all species of the generic unit under consideration. Thus, in order to qualify as an apomorphy a trait had to occur in all members of the genus, but in order to qualify as a plesiomorphy for that genus it only had to appear in a single species. Accordingly, the absence of septomaxillaries and the absence of a tibial spur in *Ixalotriton* are not appropriately viewed as synapomorphies that link the taxon to any other group. The combination of four apomorphies is unique, however.

The limits of the genus *Pseudoeurycea* could be expanded to accommodate *Ixalotriton,* but for several reasons we believe that such an action would be counterproductive. First, we strongly suspect (Wake and Elias, 1983) that *Pseudoeurycea* is paraphyletic. The reason why it would be possible to expand the concept of that genus and include the new species in it is that *Pseudoeurycea* has neither unique synapomorphies nor any unique combination of synapomorphies. *Pseudoeurycea* does share one synapomorphy (single premaxillary bone) with all tropical genera except *Nyctanolis.* We expect *Pseudoeurycea* to be broken into smaller monophyletic groups as additional information becomes available, but such a move may be slow in coming because many species are poorly known and it is increasingly difficult to obtain specimens for study. Available information concerning biochemical differentiation of the species currently assigned to *Pseudoeurycea* (Maxson and Wake, 1981; Wake and Yang, unpubl.) indicates that the group is old and highly diversified, but diagnostic osteological and other morphological traits have been very difficult to identify. We know that the majority of the species of *Pseudoeurycea* lack septomaxillary bones, and some populations of *P. cephalica* lack tibial spurs, so it is not difficult to imagine a species of *Pseudoeurycea* also evolving extremely long limb bones and large hands and feet. The closest relatives of *Ixalotriton* ultimately may prove to be some (but not all) species of the paraphyletic *Pseudoeurycea* (or possibly *Nyctanolis,* another genus ambiguously associated with *Pseudoeurycea,* see Lynch and Wake, 1989). Our description of *Ixalotriton* is a stage in the anticipated subdivision of what might be termed the "*Pseudoeurycea* complex."

Very little tissue has been available for biochemical analysis (see Lynch and Wake, 1989), but some comments can be made concerning immunological analysis. Linda Maxson, using the technique of quantitative micro-complement fixation, has made some preliminary measurements of albumin differentiation in *Ixalotriton* relative to two species of *Pseudoeurycea* (*P. smithi, P. brunnata*), and single species of *Chiropterotriton* (*C. multidentatus*), *Dendrotriton* (*D. bromeliacia*), and *Bolitoglossa* (*B. rostrata*) for which antisera have been prepared. No antisera have been available for *Ixalotriton,* so all comparisons are unidirectional. The measurements of albumin immunological distance (see Maxson and Wake, 1981) from each of these antisera to *Ixalotriton* are, in order of presentation (above), 65, 65, 89, greater than 110, and 113. These are all large distances. If one accepts the current estimate from the concept of a molecular evolutionary clock that 100 immunological distance units accumulate every 55–60 million years (Maxson and Wilson, 1975), the minimal time of divergence of *Ixalotriton* from any of the above taxa is on the order of 35 million years. There are, however, immunological differences considerably greater than 65 within *Pseudoeurycea.* In a five-by-five matrix of reciprocal comparisons of *P. bellii, P. brunnata, P. cephalica, P. leprosa,* and *P. smithi,* six of the 20 entries exceeded a value of 65, and two more exceeded 60 (Maxson and Wake, 1981). However, most of the great distances involved species of *Pseudoeurycea* other than those considered here and species that are unlikely prospects as far as possible relationship to *Ixalotriton* is concerned. By contrast, comparisons to members of other genera disclosed immunological distances of from 71 (*Dendrotriton bromeliacia*) to 88 (*Chiropterotriton multidentatus*). Dr. Maxson also has provided some unpublished data for immunological comparisons of the albumin of the poorly known *Bradytriton* and *Nyctanolis.* The former is a short-limbed terrestrial species that is an unlikely relative of *Ixalotriton,* but the latter is a potential relative. Albumin immunological distances to the five reference antisera used in comparisons with *Ixalotriton* all exceeded 90 (the only measurements less than 100 were of *Bradytriton* and *Nyctanolis* to *P. brunnata*). The distance from *Ixalotriton* to *P. brunnata* is 65, but from *Nyctanolis* to *P. brunnata* is 90. There are no data for the distance between *Ixalotriton* and *Nyctanolis,* but it is very unlikely that these genera have evolved in exactly the same direction from *P. brunnata.*

*Ixalotriton* and *Nyctanolis* appear to have evolved independently toward arboreal and scansorial life in cloud forests in nuclear Central America. The relationships of *Nyctanolis* have been discussed in detail by Elias and Wake (1983) and Wake and Elias (1983), who concluded that the genus is the sister-group of the remainder of the supergenus *Bolitoglossa.* The critical character is the paired premaxillary bones of *Nyctanolis,* a plesiomorphous trait not found in any other member of the supergenus *Bolitoglossa.* It was on the basis of this character that Wake and Elias (1983) fixed the root of the cladogram for the supergenus. The character is relatively complex and well understood. But there are also other reasons for thinking that *Nyctanolis* might be an early derivative of the ancestral stock. It has a poorly differentiated tail-breakage region and a large, stout, generalized skull. Several osteological features differentiate *Ixalotriton* from *Nyctanolis.* Not only is the premaxillary bone of *Ixalotriton* single, but the premaxillary region of the skull has a different construction from that of *Nyctanolis.* In *Ixalatriton* the frontal processes are close together and the internasal fontanelle is small. The hyobranchial apparatus and the tail base region of

*Ixalotriton* are more similar to structure in *Pseudoeurycea* than in *Nyctanolis,* and although the limbs, hands, and feet of *Ixalotriton* and *Nyctanolis* are rather similar in overall structure, *Ixalotriton* lacks a tibial spur. Accordingly, we believe that ecologically driven convergence is the most likely reason for the general morphological and ecological similarity of the genera. The alternative to this interpretation is a sister-group arrangement for *Ixalotriton* and *Nyctanolis,* based solely on the limb characters, and this would require a reversal of the premaxillary character in *Nyctanolis* (see also discussion of relationships in Lynch and Wake, 1989).

Nuclear Central America has a remarkably diverse salamander fauna, including four endemic genera (*Nyctanolis, Bradytriton, Dendrotriton,* and *Ixalotriton*), as well as representatives of *Oedipina, Bolitoglossa* (both alpha and beta assemblages), *Pseudoeurycea,* and *Nototriton.* It clearly has been an important area, not only of diversification and adaptive radiation, but also of survival of what increasingly appear to be ancient lineages (Wake and Lynch, 1976; Wake, 1987).

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During the last decade and a half many individuals have assisted us in our quest for information concerning the biology of *Ixalotriton niger.* However, none were more responsible for the initial discovery and early period of study of this species than Dr. Charles A. Ely and Jan Ely, Fort Hays State University, Hays, Kansas. Their unselfish willingness to include a fledgling undergraduate herpetologist (J.D. Johnson) in their Mexican ornithological expeditions was one of those actions that determines the direction of a person's life. The friendship that originated during those years is cherished. We are honored to dedicate this description of a new species of salamander to Chuck and Jan Ely.

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# TWO NEW SPECIES OF *PSEUDOEURYCEA* (AMPHIBIA: CAUDATA) FROM OAXACA, MEXICO

JAMES F. LYNCH[1] AND DAVID B. WAKE[2]

**ABSTRACT.** *Pseudoeurycea saltator* and *P. parva* are described from the mountains of Oaxaca, in southern Mexico. These new species are small, arboreal forms that inhabit bromeliads in two widely separated areas of cloud forest on opposite sites of the Isthmus of Tehuantepec. Morphological and protein comparisons suggest that although the two new forms are similar in external morphology, they are distinct species and are only distantly related to other *Pseudoeurycea.* Discovery of these new taxa complicates interpretaion of cladistic relationships among Middle American plethodontid salamanders of the genera *Pseudoeurycea, Ixalotriton,* and *Nyctanolis.*

**RESUMEN.** Se provee la descripción de *Pseudoeurycea saltator* y *P. parva,* de las montañas de Oaxaca, en el sur de México. Estas neuvas especies son pequeñas formas arbóreas que viven en bromelias en dos áreas ampliamente separadas de bosque nublado en lados opuestos del Istmo de Tehuantepec. Comparaciones morfológicas y de proteínas sugieren que, aunque similares en morfología externa, estas dos formas son especies diferentes, lejanamente relacionadas con otras *Pseudoeurycea.* El descubrimiento de estos nuevos taxa complica la interpretación de las relaciones cladisticas de las salamandras plethodóntidas de los géneros *Pseudoeurycea, Ixalotriton,* y *Nyctanolis.*

## INTRODUCTION

With 24 described species, *Pseudoeurycea* ranks second only to *Bolitoglossa* (68 species) in species diversity among the 12 neotropical genera of the salamander family Plethodontidae (Wake and Lynch, 1976; Wake and Elias, 1983). Whereas *Bolitoglossa* occurs from sea level to nearly 3,000 m elevation in humid habitats throughout the New World tropics, *Pseudoeurycea* is restricted to Mexico and Guatemala, and with few exceptions its species occur only above 1,200 m (Fig. 1). *Pseudoeurycea* can be abundant locally, but most species have limited geographic ranges. Consequently, discovery of new taxa can be expected as more mountain ranges become accessible (*e.g.,* Regal, 1966; Bogert, 1967; Lynch *et al.,* 1983; Wake *et al.,* 1989).

Here we describe two distinctive new plethodontid species that we tentatively assign to the genus *Pseudoeurycea.* Whereas these new forms complicate the systematics of an already problematic genus (Wake and Lynch, 1976; Maxson and Wake, 1981; Elias and Wake, 1983; Wake and Elias, 1983; Wake and Johnson, 1989), they also shed new light on the evolutionary, ecological, and biogeographic relationships among the species groups of *Pseudoeurycea,* and between that genus and its closest relatives, *Dendrotriton, Ixalotriton,* and *Nyctanolis.* We first describe the new species, and then discuss their relationships.

## SPECIES ACCOUNTS

### *Pseudoeurycea saltator* new species

Figure 2

**HOLOTYPE.** MVZ 131102, an adult male collected under the bark of a fallen log in cloud forest just west of highway 175, 16 km (by road) S Vista Hermosa, Oaxaca, Mexico (1,970 m), November 21, 1974 by D.B. Wake, J.F. Lynch, and T.J. Papenfuss.

**PARATYPES.** MVZ 112227–37, 114398, 132876–80, 147259–63 (147260 is cleared and stained), 162283 (23 specimens) all within 1 km of the holotype (1,950–2,050 m) on W side of highway 175; University of Kansas (KU) 136478–99, 136512 (23 specimens) along highway 175, 4–15 km S Vista Hermosa, Oaxaca, Mexico (1,580–1,970 m); University of Texas at Arlington (UTA) A-2869–70 (2 specimens) 27 mi [= 43 km] S Valle Nacional; UTA A-3593 25 km S Valle Nacional; Natural History Museum of Los Angeles County (LACM) 137514, same data as holotype.

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[1] Smithsonian Environmental Research Center, Edgewater, Maryland 21037.

[2] Museum of Vertebrate Zoology, University of California, Berkeley, California 94720; Research Associate in Herpetology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

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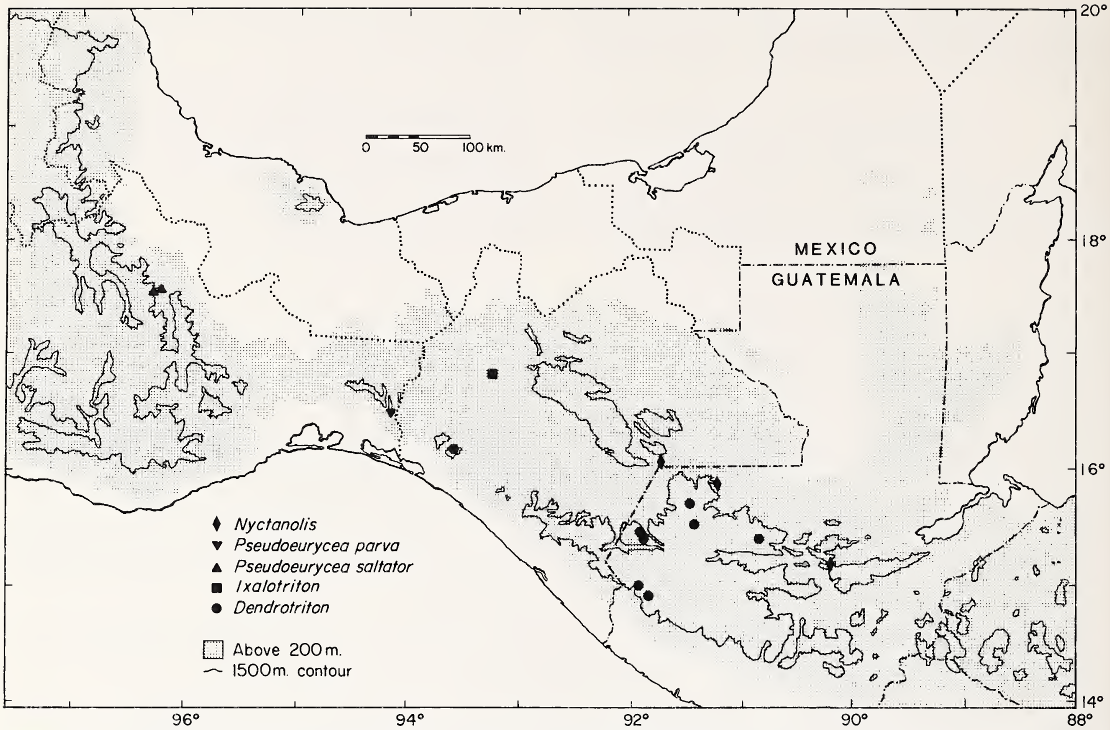

**Figure 1.** Southern Mexico and Guatemala with the distribution indicated of the two species of *Pseudoeurycea* described in this paper. All known localities for the genera *Nyctanolis, Ixalotriton,* and *Dendrotriton,* which are potential relatives of these two new species, are also indicated.

**DIAGNOSIS.** *Pseudoeurycea saltator* is one of the smallest species in the genus. Standard length (SL), the distance from the snout to the posterior angle of the vent, is generally less than 45 mm (maximum = 45 mm for males, 48 mm for females; n = 42). In its gracile external proportions and dorsally striped color pattern, *P. saltator* somewhat resembles *P. longicauda* and *P. juarezi.* The former species, which is restricted to western portions of the Transverse Volcanic Range of central Mexico (Lynch *et al.,* 1983), is much larger than *P. saltator* (males to 62 mm, females to 65 mm) and has relatively shorter limbs (combined length of the fore limb and hind limb divided by the SL averages 0.48 in *P. longicauda* vs. 0.56 in *P. saltator*). Both *P. saltator* and *P. longicauda* have long tails for the genus (in both species, mean ratio of tail length divided by SL is greater than 1.0 in adults of average SL). Compared with *P. juarezi,* which occurs at higher elevations (2,200–2,900 m) just south of the range of *P. saltator,* the new species is smaller (median SL of the largest third of our sample = 44 mm vs. 49 mm for *P. juarezi*) and has a relatively longer tail (relative tail length = 1.05 vs. 0.96 for *P. juarezi*), more vomerine teeth (projected mean at a common SL of 45 mm = 28 vs. 23 for *P. juarezi*), and more maxillary + premaxillary teeth (projected mean at SL of 45 mm = 86 vs. 78 for *P. juarezi*). The new species also differs from *P. juarezi* in color pattern. *Pseudoeurycea saltator* has a uniformly dark gray dorsal ground color that is invariably overlain by a paler mid-dorsal stripe. A diagnostic feature of the color pattern of all adults and subadults is the presence of conspicuous white or cream-colored pigmentation at the tip of the tail. In contrast, the highly variable color pattern of *P. juarezi* includes a light dorsal ground color that is marked by conspicuous dark spots and a very irregular dorsal stripe (Regal, 1966); in addition, *P. juarezi* lacks a white tail tip. These two parapatric species differ greatly in electrophoretically determined traits of various proteins (see below). In external appearance, *P. saltator* is most similar to another newly discovered *Pseudoeurycea* that is described below. Diagnostic features separating these two taxa are listed in the description of the second species.

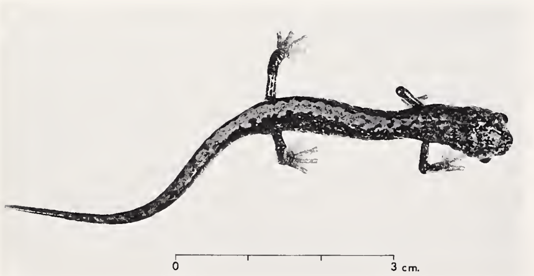

**Figure 2.** Photograph of a living *Pseudoeurycea saltator* new species (MVZ 132880), collected at the type-locality.

**MEASUREMENTS OF THE HOLOTYPE (mm).** Maximum head width, 6.0; head length (snout to gular fold), 9.2; head depth at posterior angle of jaw, 3.2; eyelid length, 2.5; eyelid width, 1.7; anterior rim of orbit to snout, 2.5; interorbital distance, 2.0; distance between vomerine teeth and parasphenoid tooth patch, 0.0; distance separating internal nares, 1.6; distance separating external nares, 2.1; snout projection beyond mandible, 0.8; snout to fore limb, 11.0; snout to anterior angle of vent, 34.1; snout to posterior angle of vent (SL), 36.8; axilla to groin, 19.1; tail length, 36.4; tail width at base, 36.4; tail depth at base, 3.0; fore limb length, 10.2; hind limb length, 11.2; width of right hand, 2.8; width of right foot, 3.7; number of premaxillary teeth, 5; number of maxillary teeth, 60; number of vomerine teeth, 28.

**COLORATION OF THE HOLOTYPE IN ALCOHOL.** The ground color is gray-black dorsally, grading to pale gray ventrally. The underside of the tail is darker than either the belly or the chin. A narrow but conspicuous mid-dorsal stripe extends from the scapular region to the tip of the tail, which is depigmented and appears white. The dorsal stripe varies in color from tan in the trunk region to gray-white on the tail. In the head region the dorsal stripe is broken into obscure flecks. Small white iridophores are scattered across the entire ventral surface but are larger and more concentrated on the chin, tail, and sides than on the belly. Coloration in life was similar, but the light iridophores were more distinct.

**VARIATION.** As in other species of *Pseudoeurycea,* the sexes of *P. saltator* overlap broadly in SL, body proportions, and coloration. However, females reach a somewhat larger overall size than do males ($P < 0.05$; Mann-Whitney U-test), and the four largest individuals in our sample of 43 are females. The basic color pattern, which varies little among individuals, features a light-colored mid-dorsal stripe on a gray-black background. The dorsal stripe typically originates in the occipital or scapular region and extends posteriorly to encompass most or all of the length of the tail. The stripe varies in color from pale cream through various shades of tan, brown, or gray and is lighter posteriorly on some individuals. The margins of the dorsal stripe vary from nearly straight to ragged or scalloped. In some individuals scattered dark concentrations of melanin are present along the margins of the stripe. A consistent feature of the color pattern is the white tail tip, which is evident in all but the smallest of the available specimens. The ventral surface is paler than the dorsum and is invariably marked by small, scattered white iridophores. These iridophores are larger and more abundant in the lateral region and on the chin and tail than on the belly.

As is typical in plethodontids, there is marked ontogenetic variation in most proportional and meristic characters. Compared to juveniles (projected to a standard SL = 30 mm), adults (projected to a standard SL = 45 mm) have more maxillary-premaxillary teeth (mean = 86 vs. 66), more vomerine teeth (mean = 28 vs. 22), relatively longer limbs (hind limb plus fore limb, divided by SL = 0.57 vs. 0.52), and relatively longer tails (tail length divided by SL = 1.05 vs. 0.81).

**OSTEOLOGY.** Information was obtained from one cleared and doubly stained male (MVZ 147260, 36.4 mm SL). The skull is compact and well ossified. The single premaxillary has a relatively broad but slender pars dentalis that bears four long, spine-like teeth; each tooth has a specialized tip consisting of a long, recurved labial cusp that extends well beyond the distinct but tiny lingual cusp and forms a minute hook-like structure. The configuration of the tooth is similar to the condition illustrated by Taylor (1941:59) for *P. unguidentis* and *P. smithi,* also Oaxacan species.

Frontal processes of the premaxilla arise independently and remain separated; these stout processes expand distally as they diverge. The processes overlap the frontal in a strong articulation, and they surround a moderately large fontanelle. The maxillaries are long and slender and bear 38 and 40 small bicuspid teeth. Septomaxillaries are absent. The nasals are relatively small, rectangular in shape, and are at most weakly articulated with the frontals and prefrontals. The well-developed prefrontal bones have areas about two-fifths those of the nasals. The nasolacrimal duct is surrounded by a distinct evacuation in the anteromedial margin of the prefrontal and a corresponding depression in the posterolateral margin of the nasal. The frontals and parietals are firmly ankylosed on the midline; there is no frontal-parietal fontanelle. A parietal "spur" is only moderately developed, and there is no ventrally directed tab. There are no crests on the otic capsules, and only one small laterally placed spine is present on one side. Vomers are weakly ankylosed for a short distance posteriorly, behind the relatively large internasal fontanelle. Preorbital processes of the vomers are long and extend beyond the body of the bone; 13–14 teeth extend beyond the lateral margins of the internal nares. The posterior vomerine tooth patches are widely separated and narrow; each contains about 65 small, bicuspid teeth. There is a well-developed, short, rod-like columella attached to the operculum.

There is an atlas, 14 trunk vertebrae (13 of them rib-bearing), 1 sacral, 2 caudosacral, and 31 caudal vertebrae. The first caudal vertebra is shorter than the second caudal or the second caudosacral and bears elongated, unbranched processes that extend sharply anteriorly. However, these processes are not especially slender or otherwise specialized as compared with the situation in other tropical plethodontids. The tail is slender. Distinct transverse processes are present on all but the small last two caudal vertebrae.

Hands and feet are typical of *Pseudoeurycea.* There is a very short, truncated tibial spur. The tarsals have the arrangement typical of the genus

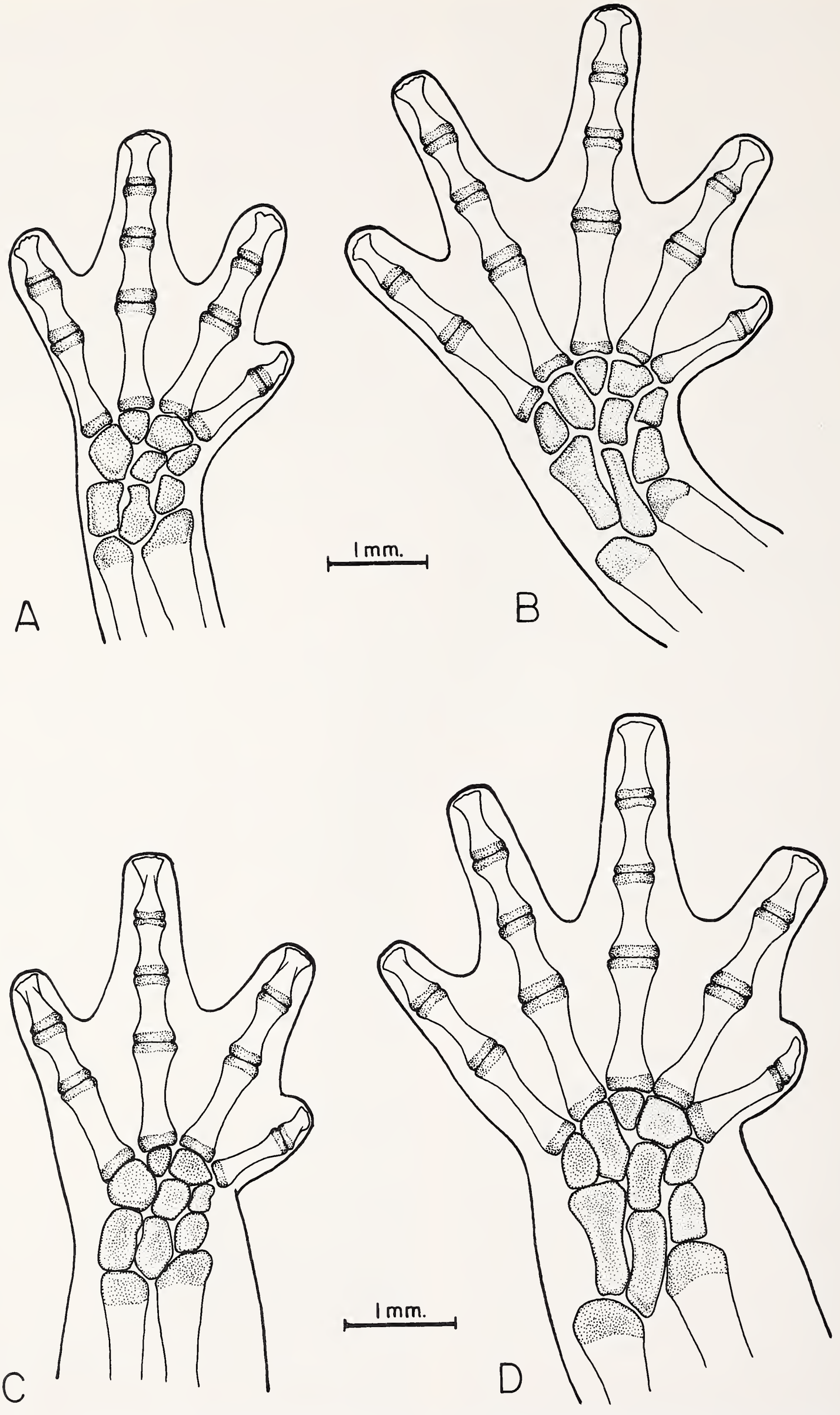

**Figure 3.** Drawings of the left hand (**A**) and left foot (**B**) of a paratype of *Pseudoeurycea saltator* new species (MVA 147260), and of the left hand (C) and left foot (**D**) of a paratype of *Pseudoeurycea parva* new species (MVZ 202294). Cartilage is stippled.

(Wake, 1966; Wake and Elias, 1983), with distal tarsal 5 being smaller than distal tarsal 4. The middle three digits of the foot are much longer than the others. Terminal phalanges are well developed and distally expanded (Fig. 3), and the distal portion is somewhat cupped. There is a small process to which the digital tendon is attached.

The hyoid apparatus is typical for the genus. No lingual cartilage is evident.

**DISTRIBUTION.** *Pseudoeurycea saltator* has been collected along a 27-km section of highway 175 that traverses the humid Caribbean-facing slope of the Sierra de Juarez, in north-central Oaxaca, Mexico (Fig. 1).

**HABITAT AND HABITS.** Most specimens have been found inside arboreal bromeliads, some as much as 8 m above the ground. A few individuals have been collected under the loose bark of downed logs. The type-locality, a steep north-facing ridge, supports a luxuriant growth of evergreen cloud forest and receives abundant precipitation even during the winter "dry" season. Extensive cloud forest is present east and west of the type-locality, but the native forest has been severely disturbed or removed by cattle ranching and coffee cultivation at the northern (*i.e.*, lower) limit of the known distribution, in the vicinity of the settlement of Vista Hermosa.

Amphibians associated with *P. saltator* at higher elevations (ca. 1,800 m) include at least five hylid (*Hyla chaneque, H. dendroscarta, H. mixe, Ptychohyla ignicolor*) and leptodactylid (*Eleutherodactylus* sp.) frogs and three species of plethodontid salamanders (*Nototriton adelos, Chiropterotriton* sp., *Thorius* sp.), all cloud-forest endemics. At the lower limit of its distribution, in the vicinity of Vista Hermosa (ca. 1,500 m elevation), *P. saltator* occurs with the same *Chiropterotriton*, a fully-webbed species of *Bolitoglossa* of the *rufescens–occidentalis* complex, a *Pseudoeurycea* tentatively identified as *P. werleri*, an unidentified species of *Thorius*, and at least seven species of hylids (*Agalychnis moreleti, Anotheca spinosa, Hyla arborescandens, H. dendroscarta, H. echinata, Ptychohyla ignicolor, P. leonhardschultzei*).

In comparison with other members of the genus, *P. saltator* is active and fast-moving. The specific name saltator is Latin for leaper or dancer and refers to the unusual ability of this species to jump when attempting to elude capture. To our knowledge, the only other tropical plethodontids that combine rapid locomotion and well-developed jumping abilities are members of two recently discovered monotypic genera, *Nyctanolis* (Elias and Wake, 1983) and *Ixalotriton* (Wake and Johnson, 1989).

## *Pseudoeurycea parva* new species

Figure 4

**HOLOTYPE.** MVZ 196101, an adult male collected by Ken Lucas inside an arboreal bromeliad on a ridge SE Cerro Baul, 21 km W Rizo de Oro, Chiapas, Mexico (ca. 1,600 m). The type-locality is just within the eastern border of the state of Oaxaca.

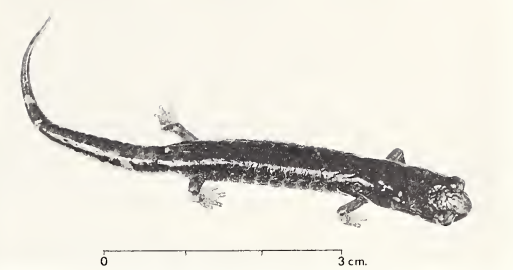

**Figure 4.** Photograph of a living *Pseudoeurycea parva* new species (MVZ 194330), collected at the type-locality.

**PARATYPES.** MVZ 196102, 196444–45 (3 specimens), 202294 (cleared and stained) same locality as holotype; MVZ 163823–25, 177823–24 (5 specimens), 16.8 km (by rd) NW Rizo de Oro (1,650–1,860 m); MVZ 194330–31 (2 specimens), Cerro Baul, 37 km (by rd) W Rizo de Oro; California Academy of Sciences (CAS) 164157–62 (6 specimens), Cerro Baul, 19 km W Rizo de Oro; LACM 137513, same locality as holotype.

**DIAGNOSIS.** This is the smallest known member of the genus. None of the 17 available specimens exceeds 40 mm SL, and all individuals with SL greater than 35 mm appear to be sexually mature. The combination of small size and a distinctive color pattern (brown dorsal stripe and lichenous white spots on the tail) easily separates this species from all other *Pseudoeurycea*, except *P. saltator*. Compared with the latter species, *P. parva* is smaller (median SL of the largest third of the sample = 39 mm in *P. parva* vs. 44 mm in *P. saltator*) and has a proportionately shorter tail (tail length projected to a common SL of 42 mm = 0.93 SL in *P. parva* vs. 1.02 SL in *P. saltator*). About half the specimens of *P. parva* lack a dorsal stripe, and when present the stripe is more obscure than in *P. saltator*. In the latter species, the dorsal pattern is formed by a heavily pigmented swath of iridophores; in contrast, the dorsal pattern of *P. parva* results from reduction in the density of melanin pigmentation in the mid-dorsal region. While *P. parva* lacks the diagnostic white tail tip found in *P. saltator*, most individuals possess conspicuous white or tan iridophore patches along the tail. There is often a pale patch on the rostrum.

In general appearance and ecology, *P. parva* somewhat resembles an oversized *Dendrotriton* (see also Wake and Elias, 1983) but differs from members of that genus in possessing prefrontal bones (see below, Osteology) and in lacking enlarged nostrils in both the juvenile and adult stages (Lynch and Wake, 1975). Both *P. parva* and *P. saltator* share some morphological and behavioral similarities with two recently discovered monotypic genera, *Nyctanolis* (Wake and Elias, 1983) and *Ixalo-*

*triton* (Wake and Johnson, 1989). However, the mosaic of similarities and differences argues against inclusion of *P. saltator* in either genus in the absence of more definitive evidence (see Discussion). We tentatively assign both new Oaxacan species to the genus *Pseudoeurycea* based on their generalized body proportions, configuration of the toes (middle digits are markedly longer than the outer ones), and retention of primitive skeletal features (see below, Osteology).

**MEASUREMENTS OF THE HOLOTYPE (mm).** Maximum head width, 6.4; head length, 9.3; depth at posterior angle of jaw, 3.1; eyelid length, 2.7; eyelid width, 1.5; anterior rim of orbit to snout, 2.9; interorbital distance, 2.5; distance between vomerine teeth and parasphenoid tooth patch, 0.1; snout to insertion of fore limb, 11.7; distance separating internal nares, 2.1; distance separating external nares, 2.4; snout projection beyond mandible, 0.9; snout to anterior angle of vent, 35.8; snout to posterior angle of vent (SL), 38.1; axilla to groin, 20.4; tail length, 38.9; tail width at base, 3.3; tail depth at base, 3.2; width of right hand, 3.1; width of right foot, 4.3; number of premaxillary teeth, 2; number of maxillary teeth, 80; number of vomerine teeth, 30.

**COLORATION OF THE HOLOTYPE IN ALCOHOL.** The ground color is dark gray-brown; the mid-dorsal region is lightened, forming an indistinct medium-brown stripe. The mid-dorsal stripe has a "dirty" appearance, due to a suffusion of small melanophores over unpigmented tissue. The dorsal stripe extends over the length of the tail, where it is overlain by large, scattered white iridophore patches. The belly is pale gray with scattered inconspicuous white flecks. Larger, more abundant white flecks are present in the lateral region of the trunk. The ventral surface of the tail is darker than the belly and has fewer iridophores. The chin is cream-colored, with a suffusion of tiny melanophores. The holotype, an adult male, possesses a well-developed kidney-shaped mental gland whose long axis is parallel to the anterior mandibular margin.

**VARIATION.** The dorsal ground color is dark brown or gray-brown in all specimens, but there is considerable individual variation in both the degree of development and the coloration of the mid-dorsal stripe. Some animals have a well-defined, contrasting stripe, others have only a slight reduction in the darkness of the ground coloration in the mid-dorsal region, and a few lack any dorsal pattern. Where present, the dorsal stripe varies in color from creamy white to dark brown, apparently depending on the degree of melanin reduction. Most individuals have at least a few conspicuous lichenous white spots scattered over the tail, but these spots vary in size and abundance. In general, individuals with reduced melanism in the mid-dorsal region also tend to be depigmented on the snout, parietal area, and limb bases. A suffusion of tiny white iridophores is invariably present on the venter, and somewhat larger white iridophores are concentrated in the lateral region of the trunk.

Sexual dimorphism is not evident in our limited sample, but there is statistically significant (determined according to methods of Lynch and Wake, 1975) ontogenetic variation in most proportional and meristic characters. Compared with standardized juveniles (character values projected to a common SL = 25 mm), standardized adults (projected to a common SL = 40 mm) have more maxillary + premaxillary teeth (80 vs. 60), more vomerine teeth (50 vs. 28), relatively longer limbs (combined length of fore limb and hind limb, divided by SL = 0.54 vs. 0.45), and relatively longer tails (tail length divided by SL = 0.91 vs. 0.62).

**OSTEOLOGY.** Information has been obtained from a cleared and stained adult female MVZ 202294 (40 mm SL). The skull is well developed, and the articulations are generally extensive and firm. The relatively stout premaxillary bone has a relatively broad, undivided pars dentalis that carries 6 bicuspid teeth. The latter are of moderate size (larger than the maxillary teeth) but are unspecialized in morphology. Frontal processes arise separately and remain separated, but they lie close together and enclose a narrow fontanelle. The processes are expanded distally, where they overlap the frontals in a firm articulation. The long and slender maxillary bones carry 32 and 33 small bicuspid teeth. These bones are rather firmly articulated to the premaxilla, the nasals, and the prefrontals. The nasals are broadly triangular in shape and of moderate size. Only a posterior tab overlaps the frontal. Septomaxillaries are absent. The prefrontals are somewhat elongate and articulate firmly with both the maxillaries and the frontals. Each prefrontal is about one-third the area of a nasal bone. The nasolacrimal duct passes between the nasal, prefrontal, and maxilla, and each bone is somewhat evacuated along the relevant margin, especially the prefrontal. Frontals and parietals are moderately ankylosed on the midline; there is only an extremely small frontal-parietal fontanelle. The parietal "spur" is only modestly developed, and there is no ventrally directed tab. Small lateral otic crests are present. Squamosals are notably large and are firmly articulated to the otic capsule. The vomers are barely ankylosed to each other posteriorly, and anteriorly the widely separated bones embrace a moderately large internasal fontanelle. Each of the long preorbital processes bears 13 teeth, which extend to the lateral margin of the internal nares. The posterior vomerine patches are narrow and well separated, and each bears about 45–50 small bicuspid teeth. The operculum bears a distinct, but very small, rod-like columella.

There is an atlas, 14 trunk vertebrae (13 of them rib-bearing), 1 sacral, 2 caudosacral, and 30 caudal vertebrae. The first caudal vertebra is weakly specialized for tail autotomy. It is only slightly shorter than the neighboring vertebrae on each side, and its transverse processes are shorter than those on

Table 1. Samples used in electrophoretic study of proteins.

| Sample number | Species | Locality |
|---|---|---|
| 1 | *P. brunnata* | San Marcos, Guatemala |
| 2 | *P. goebeli* | San Marcos, Guatemala |
| 3 | *P. juarezi* | 52 km NE Guelateo, Oaxaca, Mexico |
| 4 | *P. rex* | San Marcos, Guatemala |
| 5 | *P. rex* | Cerro Mozotal, Chiapas, Mexico |
| 6 | *P. smithi* | Cerro San Felipe, Oaxaca, Mexico |
| 7 | *D. bromeliacia* | San Marcos, Guatemala |
| 8 | *N. pernix* | Finca Chiblac, Huehuetenango, Guatemala |
| 9 | *I. niger* | 12 km N Berriozabal, Chiapas, Mexico |
| 10 | *P. saltator* | 65 km NE Guelateo, Oaxaca, Mexico |
| 11 | *P. parva* | Cerro Baul, 16.8 km NW Rizo de Oro, Oaxaca, Mexico |

the first few caudal vertebrae, an unusual condition. Transverse processes of the first caudal vertebra are only slightly swept forward from near the anterior end of the vertebra. Transverse processes are distinct on all but the last two, tiny caudal vertebrae.

The hands and feet are typical for *Pseudoeurycea,* except that there is no sign of a tibial spur. Terminal phalanges have moderate distal expansion (Fig. 3).

The hyobranchial apparatus is generally typical of the genus, but there is a distinct, well-developed lingual cartilage on the basibranchial.

**RANGE.** *Pseudoeurycea parva* has been collected only on and around Cerro Baul, a relatively isolated 2,000-m peak that lies along the continental divide just east of the Isthmus of Tehuantepec (Fig. 1). The cluster of known localities is in easternmost Oaxaca, 5–10 km west of the state border with Chiapas. Access to the area is from Chiapas, via the Pan-American highway and a rough track from the settlement of Rizo de Oro. Topographic maps indicate the existence of poorly explored montane areas, some of them higher and more extensive than Cerro Baul, just west of the type-locality. Assuming these uplands also support cloud forest, *P. parva* may have a somewhat larger range than present records indicate. Nevertheless, the low-lying, subhumid Isthmus of Tehuantepec, less than 25 km W of Cerro Baul, constitutes a major distributional barrier (Fig. 1). East of the type-locality, elevations drop below 1,500 m for nearly 50 km, before rising to 2,000 m at Cerro Tres Picos, near Tonalá, Chiapas. The salamander fauna at Cerro Tres Picos includes an endemic *Dendrotriton* (*D. megarhinus*) and an undescribed large *Bolitoglossa* of the *franklini* species-group (Wake and Lynch, 1982), but *P. parva* has not been found there.

**HABITAT AND HABITS.** All specimens of *P. parva* have been collected inside arboreal bromeliads within cloud forest at elevations ranging from 1,500 to 1,900 m. The large tank-type bromeliads used by the species have been identified as species of *Vriesia* and *Tillandsia* (D. Breedlove, pers. comm.). The only other salamander reported from Cerro Baul, a small *Bolitoglossa* of the *rufescens–occidentalis* group, also occurs inside arboreal bromeliads. The specific name *parva* is a Latin word meaning small.

## PROTEIN COMPARISONS

### METHODS

Both *P. parva* and *P. saltator* are distinctive morphologically, and their recognition as valid species does not depend on biochemical data. However, we have employed starch-gel electrophoresis of proteins as an independent means for assessing the degree of genetic differentiation of the two new species. In the future we hope to address problems of paraphyly (and possibly polyphyly) within *Pseudoeurycea* (Wake and Lynch, 1976; Maxson and Wake, 1981; Wake and Elias, 1983). Here, we consider three narrower questions. (1) Are *P. saltator* and *P. parva* close phyletic relatives? (2) Which other species of *pseudoeurycea* are most closely related to the two new species? (3) Does discovery of *P. parva* and *P. saltator* provide insight into the cladistic relationships among *Pseudoeurycea, Ixalotriton, Nyctanosis,* and *Dendrotriton*?

The procedures we employed for study of proteins have been described in detail elsewhere (Lynch *et al.,* 1977, 1983; Wake and Lynch, 1982). Briefly, we used horizontal starch-gel electrophoresis to analyze variation in 13 proteins in the two new species and in five described species of *Pseudoeurycea* (*P. brunnata, P. goebeli, P. juarezi, P. rex, P. smithi*), one species of *Dendrotriton* (*D. bromeliacia*), *Nyctanolis pernix,* and *Ixalotriton niger* (Table 1). An additional four proteins were analyzed for some taxa. Only two specimens from each population were used for most comparisons. The various taxa are sufficiently well differentiated that even small samples should provide useful information (Gorman and Renzi, 1979). Indeed, they are so distant from one another cladistically that they have few similarities, and even these should be considered suspect. A practical difficulty is that so many cross comparisons are required that tissue extracts are often exhausted before questions of protein identity are resolved.

Table 2. Proteins and conditions of analysis.

| Enzyme | Enzyme commission number | Locus | Buffer | Voltage and time run |
|---|---|---|---|---|
| Phosphogluconate dehydrogenase | 1.1.1.44 | pgdh | Tris maleate with NADP in gel | 100 V (3.5 h) |
| Adenosine deaminase | 3.5.4.4 | ada | Tris maleate with NADP in gel | 100 V (3.5 h) |
| Glycerol-3-phosphate dehydrogenase | 1.1.1.8 | gpd | Tris maleate with NADP in gel | 100 V (3.5 h) |
| Isocitrate dehydrogenase | 1.1.1.42 | icdh-1,2 | Tris citrate, pH 8.0 | 130 V (4 h) |
| Mannose phosphate isomerase | 5.3.1.8 | mpi | Tris citrate, pH 8.0 | 130 V (4 h) |
| Iditol dehydrogenase | 1.1.1.14 | iddh | Tris citrate, pH 8.0 | 130 V (4 h) |
| Phosphoglucomutase | 2.7.5.1 | pgm-1,2 | Tris citrate, pH 8.0 | 130 V (4 h) |
| Phosphoglucose isomerase | 5.3.1.9 | pgi | Tris citrate, pH 7.0 | 180 V (3 h) |
| Leucine aminopeptidase | 3.4.11.1 | lap | Tris citrate, pH 7.0 | 180 V (3 h) |
| Malate dehydrogenase | 1.1.1.37 | mdh-1,2 | Tris citrate, pH 7.0 | 180 V (3 h) |
| Aspartate aminotransferase | 2.6.1.1 | aat | LiOH | 300 V (3 h) |
| Tripeptide aminopeptidase | 3.4.11.4 | pep-b | LiOH | 300 V (3 h) |
| Dipeptidase | 3.4.13.11 | pep-c | LiOH | 300 V (3 h) |
| Lactate dehydrogenase | 1.1.1.27 | ldh | Poulik | 250 V (3 h) |

## RESULTS

The comparison of 13 proteins yielded 70 presumptive genetic alleles (x = 5.4 per locus); the comparison of 17 proteins yielded 101 alleles (x = 5.9 per locus), but there were difficulties in accurately scoring the four additional proteins in some samples. The following discussion is based on the results of the more reliable 13-locus study, except where otherwise noted (Tables 2 and 3). We fully realize that this is too low a number of proteins to be of critical value in determining phylogenetic pat-

Table 3. Allele frequencies for 13 allozyme loci. Lowercase letters in the body of the table refer to electrophoretically distinguishable alleles. For abbreviations see Table 2.

| | Species sample number (see Table 1) | | | | | | |
|---|---|---|---|---|---|---|---|
| Locus | 1 (n = 2) | 2 (n = 2) | 3 (n = 2) | 4 (n = 2) | 5 (n = 3) | 6 (n = 2) | 7 (n = 2) |
| pgdh | d (1.00) | b (1.00) | c (0.250)<br>d (0.750) | c (0.750)<br>d (0.250) | c (0.333)<br>d (0.667) | b (1.00) | e (1.00) |
| icdh-1 | c (1.00) | h (0.750)<br>i (0.250) | f (1.00) | g (0.750)<br>h (0.250) | h (0.333)<br>i (0.667) | d (1.00) | a (1.00) |
| icdh-2 | a (1.00) | b (1.00) | b (1.00) | b (1.00) | b (1.00) | a (1.00) | a (1.00) |
| mpi | b (1.00) | b (1.00) | a (0.250)<br>b (0.750) | c (1.00) | a (0.167)<br>b (0.833) | b (1.00) | d (1.00) |
| iddh | d (1.00) | e (1.00) | b (1.00) | e (1.00) | c (1.00) | e (1.00) | e (1.00) |
| pgm-1 | b (1.00) | d (1.00) | c (1.00) | b (1.00) | b (1.00) | b (1.00) | b (1.00) |
| pgm-2 | c (1.00) | d (1.00) | b (1.00) | c (1.00) | c (1.00) | c (1.00) | c (1.00) |
| pgi | d (1.00) | d (1.00) | a (0.250)<br>b (0.750) | d (1.00) | d (1.00) | d (1.00) | b (1.00) |
| lap | c (1.00) | d (1.00) | a (0.250)<br>c (0.750) | c (1.00) | c (1.00) | b (1.00) | f (1.00) |
| aat | e (1.00) | f (1.00) | e (1.00) | f (1.00) | f (1.00) | e (1.00) | c (1.00) |
| pep-b | b (1.00) | a (0.250)<br>c (0.750) | c (0.750)<br>d (0.250) | b (1.00) | b (1.00) | b (1.00) | c (1.00) |
| pep-c | b (1.00) | c (0.250)<br>e (0.500)<br>g (0.250) | c (1.00) | d (0.500)<br>f (0.500) | c (0.667)<br>e (0.167)<br>g (0.167) | e (1.00) | g (1.00) |
| ldh | c (1.00) | c (1.00) | b (0.250)<br>c (0.750) | f (1.00) | e (1.00) | c (1.00) | b (1.00) |

terns. However, the data demonstrate the distinctiveness of the species and serve to generate hypotheses of relationship. For practical reasons of comparison with the now-extensive literature on protein evolution in salamanders, we present Nei genetic distances, but we recognize that at the levels of differentiation we have found, any distant measure has little reliability as an exact measure.

The smallest value in the genetic distance matrix ($D_N = 0.3$; 3 fixed allelic differences) separates two geographically isolated populations of *P. rex.* The smallest $D_N$ value for between-species comparisons ($D_N = 0.5$; 5 fixed allelic differences) separates *P. brunnata* and *P. smithi.* At the opposite extreme, several values exceed $D_N = 1.5$, the maximum being 4.1 (12 fixed allelic differences) between *P. goebeli* and *P. parva.* The degree of genetic differentiation between *P. parva* and *P. saltator* ($D_N = 0.8$; 6 fixed allelic differences) is substantial in comparison to other salamander genera (Highton and Larson, 1979; Larson, 1984; Larson et al., 1981). In the 17-locus comparison, the degree of differentiation between *P. parva* and *P. saltator* increases to $D_N = 1.0$, with 10 of 17 loci having apparent fixed allelic differences. The proteins we examined of the two new species are more similar to one another than they are to any other species of *Pseudoeurycea* or to the other genera included in our comparison.

**Table 3. Extended.**

| Species sample number | | | |
|---|---|---|---|
| 8 (n = 2) | 9 (n = 2) | 10 (n = 2) | 11 (n = 2) |
| f (1.00) | a (1.00) | c (1.00) | a (1.00) |
| b (1.00) | e (1.00) | f (1.00) | b (1.00) |
| a (1.00) | a (1.00) | c (1.00) | a (1.00) |
| d (1.00) | b (1.00) | a (1.00) | a (0.500)<br>c (0.500) |
| a (1.00) | c (1.00) | d (1.00) | d (1.00) |
| d (1.00) | a (0.500)<br>b (0.500) | b (1.00) | b (1.00) |
| d (1.00) | a (1.00) | a (1.00) | a (1.00) |
| c (1.00) | b (1.00) | b (1.00) | b (1.00) |
| f (1.00) | d (1.00) | e (1.00) | b (1.00) |
| a (1.00) | a (1.00) | b (1.00) | b (0.750)<br>d (0.250) |
| c (0.500)<br>d (0.500) | c (1.00) | c (1.00) | c (0.750)<br>d (0.250) |
| c (1.00) | a (1.00) | c (1.00) | a (0.250)<br>b (0.750) |
| a (1.00) | b (1.00) | b (0.750)<br>d (0.250) | a (1.00) |

Other than *P. saltator,* the species of *Pseudoeurycea* most similar to *P. parva* is *P. brunnata* ($D_N = 1.0$; 8 fixed allelic differences); relative to *P. saltator,* the most similar species other than *P. saltator* is *P. juarezi* ($D_N = 1.0$; 10 fixed allelic differences). There is substantial asymmetry in these results in that *P. saltator* is much more differentiated from *P. brunnata* ($D_N = 1.9$; 11 fixed allelic differences) than is *P. parva.* Conversely, *P. parva* is more highly differentiated from *P. juarezi* ($D_N = 2.3$; 10 fixed allelic differences) than is *P. saltator.*

The two species that are least differentiated from *Ixalotriton* are *P. parva* ($D_N = 0.9$; 6 fixed allelic differences) and *P. saltator* ($D_N = 1.1$; 8 fixed allelic differences). *Nyctanolis* is more similar to *Ixalotriton* ($D_N = 1.3$; 9 fixed allelic differences) than are the remaining species of *Pseudoeurycea* in our sample. However, the species most similar to *Nyctanosis* is *P. parva* ($D_N = 1.1$; 9 fixed allelic differences), followed by *Ixalotriton,* then a group of 4 species of *Pseudoeurycea,* including *P. saltator* ($D_N = 1.5$–$1.6$). *Dendrotriton* differs substantially from all other taxa (minimum $D_N = 1.4$).

## DISCUSSION

As currently constituted, the genus *Pseudoeurycea* is a taxonomic category of convenience. Its species, many of which are rather generalized in morphology, share no uniquely derived osteological traits. Instead, the species assigned to *Pseudoeurycea* are characterized mainly by their lack of the derived traits that define other plethodontid genera (Wake and Elias, 1983). Electrophoretic analysis of proteins (Lynch *et al.* 1977, 1983; data presented herein; unpubl. data) and immunological studies (Maxson and Wake, 1981) indicate the existence of ancient phyletic divisions within *Pseudoeurycea,* but difficulties in obtaining fresh specimens of key taxa have made comprehensive biochemical comparisons impossible. In addition, few, if any, morphological traits are unambiguously correlated with biochemical patterns of similarity. Finally, there are a number of undescribed species that may affect the construction of new generic or subgeneric categories, as well as nominal species (*e.g., P. bellii*) that may constitute species groups.

Several species that may be related to *Pseudoeurycea* have been assigned to new genera (*Ixalotriton, Nyctanolis, Dendrotriton*) on the basis of a few rather accentuated morphological differences that may not accurately reflect cladistic relationships. Some species-groups of *Pseudoeurycea* (*sensu lato*) may be closer cladistically to these genera than they are to each other (Maxson and Wake, 1981). Our protein data suggest the possibility that one or both of the two new species may be closer to *Ixalotriton* or *Nyctanolis* than to at least some other species of *Pseudoeurycea.*

Comparative osteological information provides conflicting indications of relatedness. For example, *Dendrotriton* differs from some *Pseudoeurycea* (including the two new species) and from *Ixalotriton* and *Nyctanolis* in having septomaxillae (a plesiomorphic trait also found in certain species of *Pseudoeurycea*; see Wake and Elias, 1983), and from all species of these genera in lacking prefrontals and having large nostrils as juveniles and large openings of the olfactory sac throughout life (synapomorphies). *Nyctanolis* has divided premaxillary bones, an attached lingual cartilage, and tibial spurs, all plesiomorphic traits. All other genera of tropical plethodontid salamanders have a single premaxillary bone, a synapomorphy (Elias and Wake, 1983). Free lingual cartilages (an apomorphy) are found in *Ixalotriton, Dendrotriton,* and some *Pseudoeurycea,* including *P. parva,* but lingual cartilages are absent (another apomorphy that may be derived from the free lingual cartilage or may be independent of it) in other *Pseudoeurycea,* including *P. saltator.* Tibial spurs are present in most species of *Pseudoeurycea,* including *P. saltator,* but are absent (an apomorphy) in *Dendrotriton, Ixalotriton,* and *P. parva.* In one very specialized and apomorphic trait, the possession of enlarged, hook-like premaxillary teeth (Taylor, 1941), *P. saltator* differs from *P. parva* and all other neotropical salamanders except *P. smithi* and *P. unguidentis,* two species from northern Oaxaca.

Thus, while the protein evidence favors a hypothesis of relatively close relationship between the two new species, the morphological evidence suggests that *P. saltator* is clearly aligned with *Pseudoeurycea,* whereas *P. parva* is more isolated cladistically. The latter species may be more closely related to species currently assigned to other genera (*e.g., Ixalotriton*) than to the remainder of the genus *Pseudoeurycea.*

The group of species and genera considered here may represent cladistic fragments of a basal radiation in the supergenus *Bolitoglossa.* The deep genetic differentiation of the group and the ambiguous nature of the morphological data suggest a complex pattern of mosaic evolution. As a result, it is impossible to present a well-supported cladistic hypothesis at the present time.

## HISTORICAL BIOGEOGRAPHY

Recent discoveries of new salamander species and genera in southeastern Mexico and adjacent Guatemala (*e.g.,* Lynch and Wake, 1975, 1978; Wake and Lynch, 1982; Elias and Wake, 1983; Wake and Elias, 1983; Elias, 1984; Wake and Papenfuss, 1987; Wake and Johnson, 1989), and systematic revision of known genera (Wake and Elias, 1983), have strengthened our earlier conclusion (Wake and Lynch, 1976) that the mountains of nuclear Central America and the adjacent highlands of Oaxaca are major evolutionary centers for neotropical plethodontids. However, we previously emphasized the importance of the relatively young (Pliocene-Pleistocene) volcanic highlands of nuclear Central America as centers of species proliferation (Wake and Lynch, 1976), whereas it has become increasingly evident that the ancient (pre-Cretaceous) geologic core of the region has been the site of a much older and more profound phyletic radiation. Since 1976, four new plethodontid genera (*Bradytriton, Dendrotriton, Ixalotriton, Nyctanolis*) have been discovered to be endemic to a limited area of ancient mountains in Chiapas and adjacent Guatemala; five other widespread plethodontid groups (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Nototriton, Oedipina, Pseudoeurycea*) occur in the same region, which thus contains representatives of all generic groups of plethodontids that occur anywhere in nuclear Central America (Wake and Lynch, 1976; Wake and Elias, 1983). Only the Orizaba region of Veracruz, Mexico, with seven generic-level groups (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Pseudoeurycea, Chiropterotriton, Lineatriton, Parvimolge, Thorius*) approaches the generic diversity of the plethodontid fauna of eastern Chiapas and western Guatemala. Although the precipitous Atlantic slope of Oaxaca, where *P. saltator* occurs, lies between these two major centers of endemism and diversity, the Atlantic highlands of Oaxaca are separated from nuclear Central America by the low-lying, sub-humid Isthmus of Tehuantepec. The mountains of northern Oaxaca are rich in endemic plethodontid species (Wake, 1987; Wake *et al.,* 1988), but the salamander fauna of the area is not distinctive at the generic level; five of the six generic groups that occur in northern Oaxaca (*Bolitoglossa*-alpha, *Bolitoglossa*-beta, *Pseudoeurycea, Chiropterotriton, Thorius*) also are found in the Orizaba region. The sole exception is the recently described *Nototriton adelos* Wake and Papenfuss, 1987, whose affinities lie to the southeast, in nuclear Central America.

Despite earlier views that the Isthmus of Tehuantepec was the locus of a Tertiary marine portal (*e.g.,* Stuart, 1966), geologists now believe the area has been land-positive since at least the Cretaceous (Malfait and Dinkelman, 1972). Nevertheless, the isthmian region must have formed a long-standing distributional barrier for animals that require cool, humid conditions (Halffter, 1987). Two lowland species of *Bolitoglossa* (*B. mexicana, B. rufescens*) occur on both sides of the Isthmus, but no montane species does so. Indeed, the only species-groups of high-elevation salamanders with representatives east and west of the Isthmus are the *gadovii* group of *Pseudoeurycea* (*sensu* Maxson and Wake, 1979) and, possibly, two recently described species of *Nototriton* (Papenfuss and Wake, 1987). Apart from *P. parva,* just five species of *Pseudoeurycea* range east of the Isthmus of Tehuantepec: *P. brunnata, P. expectata, P. goebeli, P. rex,* and an undescribed Guatemalan species (Wake and Lynch, 1976). All are found at high elevations (above 2,500 m) in Guatemala and easternmost Chiapas, usually in terrestrial microhabitats. Our analysis of protein data suggests that this assemblage is only distantly related to *P. saltator* and *P. parva.*

Both *P. parva* and *P. saltator* have ambiguous relationships to other *Pseudoeurycea* and to allied genera. *Pseudoeurycea parva* resembles *Dendrotriton* in habitus, and is intermediate in overall size between the largest *Dendrotriton* and the next smallest *Pseudoeurycea.* The habitat/microhabit association of *P. parva* (arboreal bromeliads in mid-elevation cloud forests) is typical of *Dendrotriton* (Wake and Lynch, 1976; Lynch and Wake, 1975, 1978) but unusual in *Pseudoeurycea,* most species of which inhabit terrestrial microhabitats at high elevations (Wake and Lynch, 1976). Three allopatric *Dendrotriton* (*D. bromeliacia, D. xolocalcae, D. megarhinus*) occupy the three known isolates of montane cloud forest along the Pacific versant between western Guatemala and the range of *P. parva,* a fact consistent with the hypothesis that both groups comprise remnants of a once continuous range. On the Atlantic versant, the ecological roles of *Dendrotriton* and *P. parva* are filled by *D. rabbi* in west-central Guatemala, *Nyctanolis* in western Guatemala and adjacent Chiapas, *Ixalotriton* in central Chiapas, and *P. saltator* in central Oaxaca. Again, the fact that none of the eight species of small to medium-sized arboreal specialists are sympatric is consistent with the hypothesis that a breakup of formerly continuous areas of cloud forest stranded ancestors of these salamanders within isolated areas of favorable habitat on the margins of the ancient core of nuclear Central America.

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# Contributions in Science

## Taxonomy of the *Cecropia*-inhabiting Ants in the *Azteca alfari* Species Group (Hymenoptera: Formicidae): Evidence for Two Broadly Sympatric Species

John T. Longino

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# TAXONOMY OF THE *CECROPIA*-INHABITING ANTS IN THE *AZTECA ALFARI* SPECIES GROUP (HYMENOPTERA: FORMICIDAE): EVIDENCE FOR TWO BROADLY SYMPATRIC SPECIES

JOHN T. LONGINO[1]

**ABSTRACT.** The numerous species of the genus *Azteca* constitute a large neotropical radiation of dolichoderine ants. All species are arboreal, nesting in external carton nests, cavities in dead trunks or branches, or in live stems. Of the latter, some exhibit obligate associations with specialized myrmecophytes. Myrmecophytic *Cecropia* trees are inhabited by several distinct species groups of *Azteca*. One of these is here defined and revised as the *Azteca alfari* species group, composed of two broadly sympatric, polytypic species: *A. alfari* sensu stricto and *A. ovaticeps*. The following new synonymy is proposed: *Azteca alfari* Emery = *A. alfaroi* race *lucidula* Forel = *A. virens* Forel = *A. alfari* subsp. *cecropiae* Forel = *A. alfari* var. *mixta* Forel = *A. alfaroi* var. *fumaticeps* Forel = *A. alfari* var. *curtiscapa* Forel = *A. foreli* race *breviscapa* Forel = *A. lynchi* Brèthes = *A. alfari* var. *argentina* Forel = *A. alfari* var. *langi* Wheeler = *A. alfari* subsp. *lucidula* var. *zonalis* Wheeler, and *Azteca ovaticeps* Forel = *A. alfari* var. *aequilata* Forel = *A. alfari* var. *aequalis* Forel = *A. alfari* subsp. *tuberosa* Forel. *Azteca alfaroi* race *lucida* Forel is raised to species, but excluded from the *A. alfari* group.

**RESUMEN.** Las hormigas dolichoderinas del género *Azteca* tienen una dispersión neotropical. Los especies son sumamente arbóreo, nidificando en panales de sustancia vegetal, en tallos secos, o en tallos verdes. Algunos de los especies que habitan tallos verdes forman asociaciones simbióticas con plantas mirmecófilas, incluyendo el género *Cecropia*. Algunos grupos-especies distintos de *Azteca* habitan arboles mirmecófilos de *Cecropia*. Aquí defino y reviso uno de estos grupos-especies, el grupo de *Azteca alfari*, compuesto de dos especies politípicos, de distribución amplia y simpátrica.

## INTRODUCTION

Ants in the dolichoderine genus *Azteca* are major elements of neotropical forest ant communities (Forel, 1899). The numerous species exhibit a variety of nesting habits, inhabiting external carton nests, dead branches, dead cores of living trees, and live branches. The species that have attracted the most attention are those that form specialized associations with myrmecophytic plants, in particular those that inhabit *Cecropia* trees (reviews in Bequaert, 1922; Wheeler, 1942; Janzen, 1969, 1973; and Buckley, 1982). Lack of adequate species-level taxonomy for the *Azteca–Cecropia* association has delayed and obscured understanding of this prominent ant–plant system. Advances are being made in the taxonomy of *Cecropia* (*e.g.* Berg, 1978a,b), and here I present a first contribution to the taxonomy of *Cecropia*-inhabiting *Azteca.*

Forel (1878) established the genus *Azteca,* basing it on the polymorphic worker caste and features of the proventriculus. The weakly chitinized integument and the reflexed proventricular sepals allied *Azteca* with the genera *Iridomyrmex, Liometopum,* and *Tapinoma.* The definition of the genus has remained essentially unchanged, and as currently recognized the genus is almost certainly a monophyletic group within the Tapinomini (S.O. Shattuck, pers. comm.). Emery (1893) provided the first and as yet only revision of *Azteca,* recognizing 25 valid names. A flurry of disconnected descriptions followed, bringing the total to 155 available names (Kempf, 1972) but no real understanding of the genus.

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[1] Department of Biological Sciences, University of California, Santa Barbara, California 93106; Research Associate, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

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Within the large genus *Azteca,* a few species are obligate inhabitants of *Cecropia* trees (Benson, 1985; Longino, 1989). These are *A. coeruleipennis* Emery, 1893, *A. constructor* Emery, 1896, *A. muelleri* Emery, 1893, *A. xanthochroa* (Roger, 1863), and *A. alfari* Emery, 1893. The latter three are species complexes with numerous infraspecific taxa. Species in the *A. alfari* complex can be distinguished from all other obligate *Cecropia* inhabitants by the lack of standing setae on the tibiae and scapes.

In this report, the *A. alfari* group is defined and revised. The species group is interpreted as a complex of two closely related, polytypic species, broadly sympatric in the Neotropics.

## MATERIALS AND METHODS

### COLLECTIONS

Collections are referred to by the following acronyms, following Arnett and Samuelson (1986).

LACM: Natural History Museum of Los Angeles County, Los Angeles, CA, USA
MCSN: Museo Civico de Storia Naturale "Giacomo Doria," Genoa, Italy
MCZC: Museum of Comparative Zoology, Cambridge, MA, USA
MHNG: Museum d'Histoire Naturelle, Geneva, Switzerland
USNM: National Museum of Natural History, Washington, DC, USA

Much of the non-type material on which this study was based is from personal, LACM, and MCZC collections. Personally collected material from Costa Rica, Colombia, and Venezuela has been deposited in LACM and national collections of the countries of origin.

### METHODS

Measurements were made at 63× magnification, with an ocular reticule, and are accurate to the nearest 0.01 mm. All measurements are presented in mm. Sculpture terminology generally follows Harris (1979). Drawings of queens and workers were made freehand using a Zeiss dissecting microscope with an eyepiece grid. Male antennae were illustrated by photographing either dry-mounted specimens or slide-mounted antennae and tracing from the projected negatives. The following characters are used:

HL: Head length (workers and queens), measured in frontal view (occipital border and anterior border of clypeus in same plane of focus) along the midline, from a point level with the posteriormost points of the occipital lobes to the anterior border of the clypeus.
HW: Head width (workers and queens), measured in frontal view across the widest portion of the head above the eyes.
SL: Scape length, not including basal neck and condyle.
EL: Eye length on longest axis.
WL: Weber's length (workers and queens), straightline distance from anteriormost point of pronotum (near pro-mesonotal suture for queens) to posteriormost point of metapleural lobe, accurate to 0.05 mm.

The following indices are reported:

CI: HW/HL
SI: SL/HW

The following setal counts are used:

GTC: Number of standing setae on second gastric (fourth abdominal) tergite exclusive of posterior row, including portion of tergite that wraps laterally to the ventral side of the abdomen. Counted on queens only. The posterior row continues up the lateral margins of the tergite (on the ventral surface of the gaster). When GTC > 5, the setae are usually somewhat symmetrically arranged on the abdominal dorsum, with fewer on the lateral portions of the tergite.
MSC: Number of standing setae on mesonotum of workers. Very fine, short setae are included in the count, and often these fine setae are only visible at particular angles and proper lighting. When more than 10 setae are present, counting is difficult and requires constant repositioning of the specimen. Counts are made up to 19 setae, after which specimens are scored as ≥20. Also, this character is subject to specimen age bias, due to rubbing and presumed progressive loss of setae.

Measurement data are presented in tabular form to aid in comparing the two species. In choosing material to measure, an attempt was made to minimize nonindependence of samples due to close genetic relatedness. Usually only one specimen per caste per colony was measured, and from at most three colonies per collecting site.

For worker measurements, a single worker was chosen from among the largest workers in a nest series. Interpretation of measurement data is difficult for the polymorphic workers of *Azteca.* There are prolonged ontogenetic and/or colony size-specific changes in worker size distribution and color (pers. obs.). Workers in incipient colonies are small and darkly pigmented. Larger and/or older colonies exhibit a great variability in color and maximum worker size, but the largest and lightest-colored workers are generally from very large colonies. Allometric head-shape change produces variable head shape both within and between colonies. These conditions make worker size and head shape poor taxonomic characters. Worker measurements are reported here to distinguish the *A. alfari* group from other species groups, rather than to differentiate species within the group.

The frequent occurrence of sympatric sibling species in the *A. alfari* group, coupled with imprecise designation and labeling of type material by early workers, has resulted in uncertainty regarding types, and occasionally syntype series consist of more than one species. I have found it necessary to make extensive use of lectotype designations to fix names and establish synonymy. For many taxa, I have designated lectotypes from what I judge to be a single nest series (based on data labels), from the available syntype material.

## EVIDENCE FOR SYMPATRIC SPECIES

*Azteca alfari* group queens can be found in large numbers colonizing *Cecropia* saplings (Longino, 1989). Prior to dominance by a single colony, each internode of a sapling may house one or more founding queens. At several sites, I have found that *A. alfari* group founding queens occur in two discrete forms: one darkly pigmented and sparsely pi-

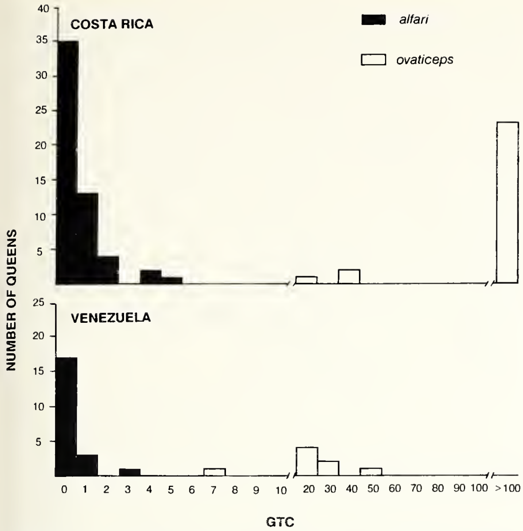
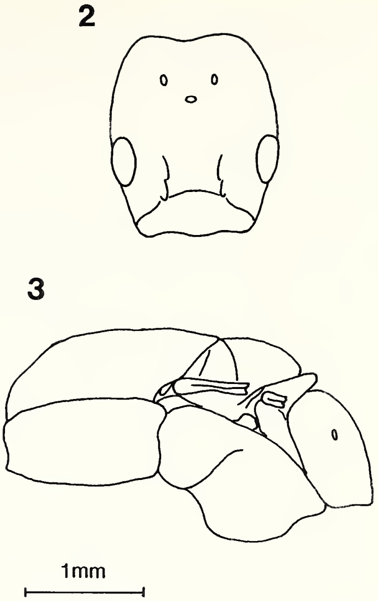


**Figure 1.** Bimodal distribution of GTC (number of setae on second gastric tergite of queens, exclusive of posterior row) for *Azteca alfari* group species. **A.** Samples of queens from throughout Costa Rica (see Material Examined under species treatments). **B.** Samples of queens from Venezuela, Estado Barinas.



**Figures 2, 3.** *Azteca ovaticeps* (syntype queen). **2.** Frontal view of head. **3.** Lateral view of mesosoma.

lose and the other lightly pigmented and densely pilose (here referred to *A. alfari* sensu stricto and *A. ovaticeps*, respectively).

In Costa Rica, a character that separates the two species is the number of standing setae on the second gastric (fourth abdominal) tergite, exclusive of the posterior row. A survey of 81 queens from localities throughout Costa Rica reveals a strongly bimodal distribution for this character (Fig. 1). For a quantitative character such as seta number, a unimodal distribution would be expected were the sample from a single panmictic population. A sample from Venezuela revealed less differentiation based on abdominal setae (Fig. 1), but queens were strongly differentiated into two forms by the presence or absence of a dense brush of setae on the clypeus (Figs. 6, 11).

That the *alfari* group is composed of two sympatric species is also suggested by Harada (1982). In her study of *Cecropia*-inhabiting ants of Brazil, she observed a "brown form" and a "black form" of *A. alfari* queens from the Manaus area. Although color is not diagnostic, *A. ovaticeps* queens are usually light to dark brown, whereas *A. alfari* queens are typically black.

Alternative explanations for dimorphism include ecotypic variation in phenotype or intraspecific genetic polymorphism. Ecotypic variation is an unlikely explanation for the two forms because of the fine spatial scale on which they co-occur. Colonies of the two species are found inhabiting adjacent trees, and saplings frequently contain queens of both species. Intraspecific genetic polymorphism cannot be ruled out, but no cases of intracolonial polymorphism have been observed, either among siblings or between colony queens and offspring. The two forms are probably non-interbreeding sympatric populations; they are different species.

## *AZTECA ALFARI* GROUP

### DIAGNOSIS (QUEEN)

*Obligate inhabitants of Cecropia trees;* head longer than wide (HL 1.50–1.72, CI 0.778–0.863), sides evenly convex, and occipital border neither broadly cordate nor deeply excavated (Fig. 2); scapes in repose fall about mid-way between upper margin of eye and occipital border (SL 0.71–0.85); eyes elliptical to somewhat reniform (EL 0.37–0.45); mandibles 7-toothed; mesosoma shape as in Figure 3; *mandibles largely nitid* with large, piligerous foveae, becoming alveolate at base; head, mesoscutum, and mesoscutellum densely and minutely punctate, dorsum of gaster minutely alveolate; body and appendages covered throughout with fine appressed pubescence; standing setae always present on dorsal and ventral surfaces of head, and on dorsum of pronotum, mesoscutum (often setae nearly absent), mesoscutellum, propodeum, petiole, and first gastric tergite; second gastric tergite always with a posterior row of setae, setae variably present anterior to this; standing setae variably present on femora, but *essentially absent on tibiae* (tibial setae, when present, restricted to the tibia apex, and rarely 1 to a few short setae irregularly placed elsewhere on the shaft); *scapes generally devoid of setae* except at apex, occasionally up to 10 short, subdecumbent setae of irregular lengths and spacing; color ranging from light brown to solid black, color generally progressing from darker to lighter in a distal direction along extremities: legs, antennae, and clypeal region of head.

## DIAGNOSIS (WORKER)

Head length of largest workers ≤1.38; head slightly longer than wide (CI 0.86–0.94), subquadrate to subtriangular (narrowed toward the mandibles); occipital border cordate to varying degree; scapes in repose fall ½ (large workers) to ⅘ (small workers) the distance between upper margin of eye and occipital border (SI 0.60–0.76); mandibles largely nitid with 8–10 teeth, depending on worker size; mesonotal profile composed of an upwardly sloping pronotum, an arched and protruding mesonotum that is often separated from the pronotum by a distinct anterior declivity, in larger workers a metanotal remnant often protruding between mesonotum and propodeum, and the propodeum with nearly level basal face and a distinct declivitous face of similar length; surface sculpture as in the queen; long-standing setae always present on the dorsum of the pronotum, mesonotum, propodeum, petiole, and gaster; scape and tibial pilosity as in the queen; color highly variable, ranging from concolorous brown, to light brown mesosoma and gaster with dark brown head, to concolorous light brown or yellow.

## COMMENTS

Of the several character systems that Emery (1893) used to differentiate *Azteca* species, those I have found most useful are queen head shape and distribution of pilosity on queens and workers. I suspect that both systems are strongly influenced by natural selection, making them good taxonomic characters because of the resulting diversification, but difficult characters for phylogeny reconstruction because of the increased likelihood of convergence.

Most of the species that inhabit carton nests either externally (*e.g. A. barbifex, A. chartifex, A. traili*) or in hollow tree trunks (*e.g. A. instabilis, A. velox*) have abundant standing setae on the scapes and legs. Pilose tibiae are probably of great utility in the manipulation of shredded plant matter used in carton construction. I suspect that tibial pilosity and carton construction are plesiomorphic in the genus. *Liometopum*, a possible outgroup for *Azteca*, exhibits both these characters. The early Miocene *Azteca alpha* Wilson (1985), one of two known fossil *Azteca*, has hairy tibiae and is very similar to any number of modern *Azteca* species (pers. obs.). Several obligate *Cecropia*-inhabiting species—*A. muelleri, A. constructor, A. xanthochroa*, and *A. coeruleipennis*—have densely pilose tibiae and, I suspect, were derived from carton-nesting species.

In contrast, there are many species that inhabit the narrow stems and branches of live plants, and these exhibit various degrees of loss of tibial and scape setae (setae on the thoracic dorsum are rarely absent). In narrow galleries, tibial setae may be an impediment, favoring their evolutionary loss. Also accompanying the stem-nesting habit is a great diversity of queen head shapes. In particular, several species exhibit extremely elongate heads with straight sides (*e.g. A. fasciata, A. longiceps*). Worker head shapes do not show nearly the elaboration that queen head shapes do. I suspect that queen head shape is under strong natural selection at the time of colony founding, influencing the kinds of stems that can be used and the speed with which they can be entered.

The *Azteca alfari* group is part of this second portion of the genus, among the stem-nesting species with bare scapes and tibiae. Close relatives include *A. emeryi* Forel and *A. foreli* Emery. *Azteca emeryi* is similar to the *A. alfari* group in many respects, the striking difference being the extremely elongate, parallel-sided head of the *A. emeryi* queen. Worker heads are also somewhat elongated. At the time of Kempf (1972), *A. emeryi* was known only from the types. I have examined the types of this species, from a *Cecropia* tree at Cachveira Juruá, Amazonas, Brazil (Ule), and a worker series, tentatively identified as *A. emeryi*, from a *Cecropia* at Cocha Totora, Departamento Madre de Dios, Peru (Davidson). The latter is the only collection out of dozens of collections of *A. alfari* group colonies in the region. I predict, given the queen head shape, that *A. emeryi* will prove to be an only occasional occupant of *Cecropia* trees and a more specialized inhabitant of some other plant genus with narrower stems. *Azteca emeryi* may best be placed as a derived member of the *A. alfari* group, but I await further knowledge of this poorly known species.

*Azteca foreli* workers are very similar to *A. alfari* group workers in pilosity, size, and head shape. The primary difference is that the mandibles of *A. foreli* are densely sculptured, with a granular or striate appearance, in contrast to the shiny mandibles of the *A. alfari* group. *Azteca foreli* is very different behaviorally, nesting in hollow live stems of a variety of canopy trees. It has the unique habit of constructing completely closed carton galleries on trunk and branch surfaces, traversing the host tree between hollow stems.

I have not considered males in the definition of the *A. alfari* group. *Azteca* males are frail, similar to workers in size, and very much smaller than queens. A cursory examination of males from a variety of *Azteca* species revealed few sources of morphological variability. The phallus is comprised of the weakly sclerotized, largely membraneous aedeagus, flanked by pick-like volsellae, subsequently flanked by the swollen basiparameres, at the tip of which are the small, triangular parameres (terminology after Snodgrass, 1941). A distinct articulation often separates the paramere and basiparamere. Tergites IX and X are absent, and there are no pygostyles. The volsellae have acute tips in some

**Table 1. Comparative measurements of *Azteca alfari* and *A. ovaticeps*. Ranges are given, followed in parentheses by median and sample size. All measurements are in mm. Characters in bold show the greatest separation between *alfari* and *ovaticeps*.**

| | Species | | | |
|---|---|---|---|---|
| | *alfari* | | *ovaticeps* | |
| Queens | | | | |
| HL | 1.51–1.69 | (1.63, 26) | 1.51–1.72 | (1.59, 19) |
| HW | 1.24–1.43 | (1.35, 26) | 1.20–1.39 | (1.32, 19) |
| SL | 0.71–0.81 | (0.77, 25)* | 0.73–0.85 | (0.80, 19) |
| EL | 0.39–0.45 | (0.43, 13) | 0.37–0.42 | (0.40, 13) |
| WL | 2.55–3.05 | (2.80, 25) | 2.70–3.15 | (2.88, 16) |
| CI | 0.778–0.856 | (0.826, 26) | 0.785–0.863 | (0.820, 19) |
| **SI** | **0.543–0.610** | **(0.573, 25)**** | **0.589–0.669** | **(0.608, 19)** |
| **GTC** | **0–5** | **(0, 80)** | **17–>100**<br>**(Costa Rica)** | **(>100, 26)** |
| | | | **2–42**<br>**(South America)** | **(14, 11)** |
| Workers | | | | |
| HL | 0.80–1.38 | (1.06, 32) | 0.87–1.29 | (1.10, 16) |
| HW | 0.72–1.21 | (0.96, 32) | 0.77–1.16 | (0.99, 16) |
| SL | 0.53–0.74 | (0.64, 24) | 0.58–0.75 | (0.71, 16) |
| CI | 0.858–0.942 | (0.905, 32) | 0.870–0.914 | (0.888, 16) |
| SI | 0.603–0.734 | (0.681, 24) | 0.632–0.763 | (0.715, 16) |
| **MSC** | **2–17** | **(8, 66)** | **10–>19** | **(>20, 40)** |

* Outlier from Panama, 0.85.

** Outlier from Mexico, 0.649.

species and are blunt to somewhat knobbed in others. *Azteca alfari* group males exhibit slightly knobbed volsellae, as do many other *Azteca* species.

*Azteca* male antennae are composed of a short trapezoidal first segment (scape), a globular second segment, and variably shaped segments 3 to 13. The first and second segments are largely bare, whereas the remaining segments are densely covered with short setae. There is both intra- and interspecific variation in the size and shape of antennal segments, particularly segment 3. Although the shape of the third antennal segment is used to differentiate species within the *alfari* group (see below), diagnostic male characters for the *alfari* group as a whole are unknown.

In *Azteca* males preserved in alcohol, I have often observed what appear to be large eversible sacs between the anus and tergite VIII and between tergites VII and VIII. These sacs are probably associated with glandular products (Hölldobler and Engel-Siegel, 1982). I speculate that elaboration of antennal structure and abdominal glands results from a reliance on chemical communication during courtship and mating, replacing structural elaboration of genitalia as a reproductive isolating mechanism or feature subject to sexual selection (cf. Eberhard, 1985). This could be examined through comparative studies of *Azteca* mating behavior and pheromone chemistry.

## SPECIES ACCOUNTS

### *Azteca alfari* Emery, 1893

Table 1

Figures 1, 4–9, 14–21, 28–32, 37–42, 47

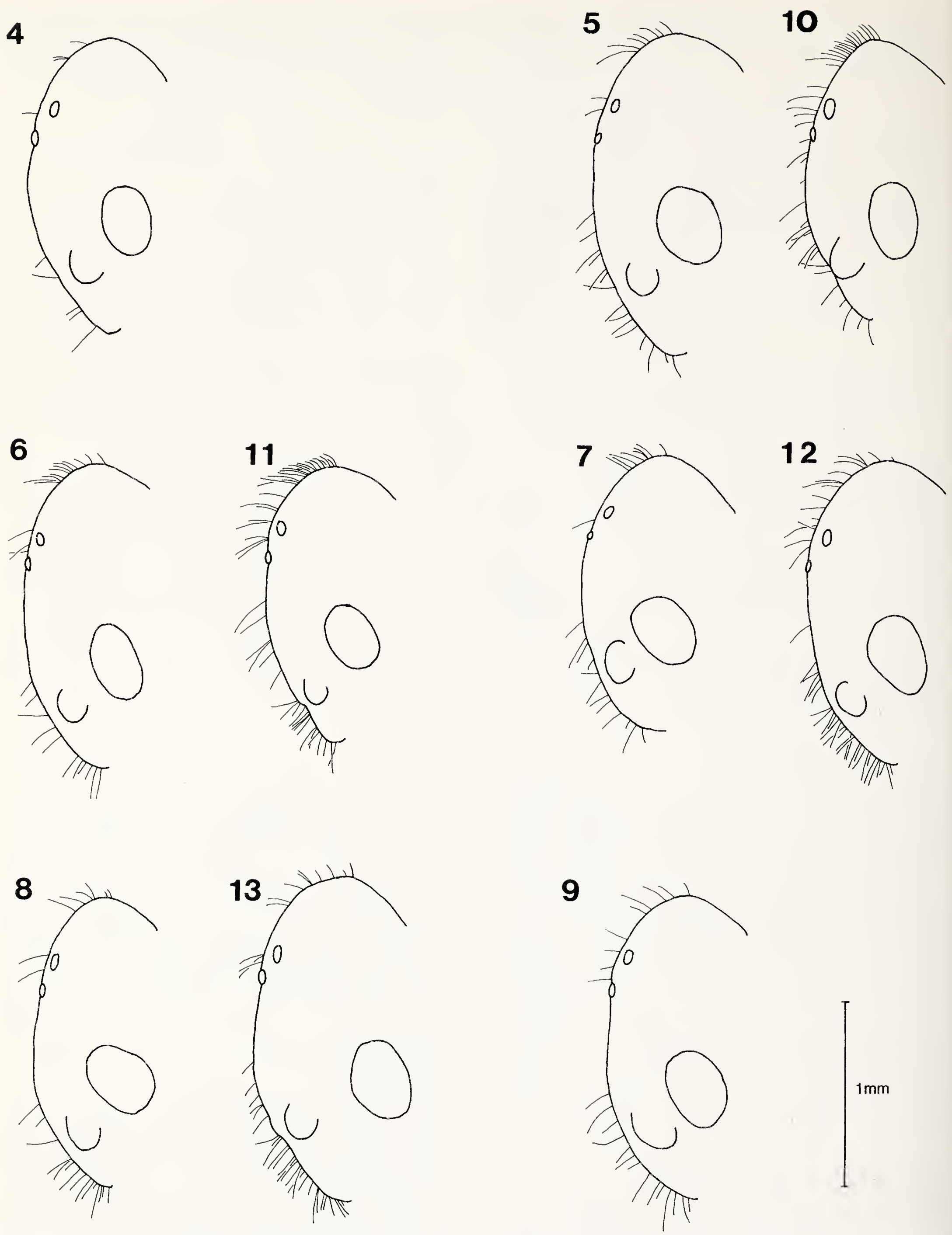
*Azteca alfari* Emery, 1893:138; syntype workers: Jiménez, Altantic slope, Costa Rica (Alfaro) [MCSN] (examined, one worker here designated as LECTOTYPE, remainder of nest series PARALECTOTYPES, other material excluded from type series).

*Azteca alfaroi* Emery; Emery, 1896:4 (description of queen).

*Azteca alfaroi* race *lucidula* Forel, 1899:113; syntype workers, queens, males: Trinidad (Urich); Guatemala, Retalhuleu (Stoll) [MHNG] NEW SYNONYMY (examined, one queen from Trinidad here designated as LECTOTYPE, remainder of nest series PARALECTOTYPES, other material excluded from type series).

*Azteca virens* Forel, 1899:115; syntype workers: Brazil, Amazonas, Pará (Göldi) [MCZC] NEW SYNONYMY (examined).

*Azteca alfari* subsp. *cecropiae* Forel, 1906:240; syntype workers: Brazil, Amazonas, Manaus (Göldi, Huber) [MHNG] NEW SYNONYMY (Huber series examined, one Huber worker here designated LECTOTYPE, other material excluded from type series).



**Figures 4–13.** *Azteca alfari* group queens, lateral view of head. Setal patterns were drawn by focusing on the midline of the head and drawing all setae that were close enough to the plane of focus to be visible as a single seta. *A. alfari:* **4,** Mexico; **5,** Costa Rica; **6,** Venezuela; **7,** Brazil, Manaus; **8,** Bolivia; **9,** Paraguay (*A. mixta* lectotype). *A. ovaticeps:* **10,** Costa Rica; **11,** Venezuela; **12,** Brazil, Pará (*A. ovaticeps* syntype); **13,** Bolivia.

*Azteca alfari* subsp. *cecropiae* Forel; Forel, 1908: 387 (description of queen, male: Brazil, Campo Besso, near São Paulo (von Ihering) [MHNG] examined).

*Azteca alfari* var. *mixta* Forel, 1908:386; syntype workers, queens, males: San Bernardino, Paraguay (Fiebrig); Brazil, São Paulo (von Ihering) [MHNG] NEW SYNONYMY (examined, one queen from Paraguay here designated LECTOTYPE, remainder of nest series PARALECTOTYPES, São Paulo series excluded from type series).

*Azteca alfaroi* var. *fumaticeps* Forel, 1909:250; syntype workers: Mexico, Buenaventura (Ross) [MHNG] NEW SYNONYMY (examined).

*Azteca alfari* var. *curtiscapa* Forel, 1912:51; syntype workers, queen: Panama (Christophersen); Costa Rica (no collector) [MHNG] NEW SYNONYMY (examined, one queen from Costa Rica here designated LECTOTYPE, remainder of nest series PARALECTOTYPES, Panama material excluded from type series).

*Azteca foreli* race *breviscapa* Forel, 1912:51 [nov. stat. of *Azteca foreli* race *championi* var. *breviscapa* Forel, 1899:112]; syntype workers: Costa Rica (Tonduz) [MCZC, USNM] NEW SYNONYMY (examined).

*Azteca alfari* var. *argentina* Forel, 1914:287; syntype workers: Argentina, Misiones, Santa Ana (Bruch) [MHNG] NEW SYNONYMY (examined).

*Azteca lynchi* Brèthes, 1914:93; syntype worker(s): Bolivia (Arribálzaga) provisional NEW SYNONYMY (not seen).

*Azteca alfari* var. *argentina* Forel; Gallardo, 1916: 115 (description of major worker and queen, not seen).

*Azteca alfari* subsp. *lynchi* Brèthes; Gallardo, 1916: 118 (lowered to subspecies).

*Azteca alfari* var. *fumaticeps* Forel; Wheeler, 1942: 218 (description of queen: Guatemala, Quirigua, 14.i.1912; and Puerto Barrios, 4.xii.1911 (Wheeler) [MCZC] examined).

*Azteca alfari* var. *langi* Wheeler, 1942:218; syntype workers, queens, males: Guayana, Kamakusa (Lang) [MCZC] NEW SYNONYMY (examined).

*Azteca alfari* subsp. *lucidula* var. *zonalis* Wheeler, 1942:222 (unavailable name); syntype workers, queens: Panama, Corozal, 21.xi.1911 (Wheeler) [MCZC] (examined).

## DIAGNOSIS (QUEEN)

*GTC* < *6;* dorsal surface of head, when viewed in profile, with setae occurring in three clusters separated by distinct gaps, one cluster on and just above the clypeus, one around the ocelli (these may be entirely absent), and one on the occiput (Figs. 4–9); clypeal setae sparse, never forming a dense brush (Figs. 4–9); mesoscutum with irregularly scattered setae to almost devoid of setae; SI generally ≤0.60; color usually black.

## COMMENTS

The identity of true *A. alfari* was problematical. The type locality appeared in Emery's revision as Jimenez, Costa Rica. Two pins of worker series were examined from MCSN. One pin held a "typus" label, and a label with "Suerre" (a site within 2 km of Jimenez) and the identification "alfaroi" (an attempted emendation of *alfari* that appeared later). The other had a "Jimenez" locality label and a separate label with the identification "*alfari*," but no typus label. The two collections were not conspecific, consisting of the two commonly microsympatric species in the *A. alfari* group. Workers from the latter series, much more than the former, resembled Emery's 1893 illustration of *A. alfari.* A worker from the Jimenez series was chosen as a lectotype of *A. alfari* sensu stricto; the remaining workers on the pin were designated paralectotypes. The Suerre collection, now identified as *A. ovaticeps,* was excluded from the types of *A. alfari.*

Designation of a lectotype queen for *A. lucidula* was necessary because one "cotype" series of workers, queens, and males from Trinidad with label "Trinidad (Urich) sans No." was *A. alfari,* whereas a second "cotype" series of workers with label "Trinidad 59" was *A. ovaticeps.* I examined a single "cotype" worker from Retalhuleu, Guatemala (Stoll), that has standing setae on scapes and legs, which excludes it from the *A. alfari* group. A queen from the Trinidad "sans No." series was designated lectotype; the remaining workers, queens, and males in this series were designated paralectotypes, and all other series excluded from the types.

Forel described *A. virens* as being similar to *A. alfari,* with *A. virens*' outstanding feature being its green color. The body was described as partly translucent, and the green color came from within, recalling the color of green caterpillars. The collection was shipped from Pará "with the green stem of a plant." I examined syntypes at MCZC that were not green and were identical to typical *A. alfari.* I conjecture that the ant specimens were sent in fluid with the stem, perhaps in a plant preservative containing glycerine and acetic acid, and so obtained their translucent nature and green color.

I examined five workers from the Huber syntype series of *A. cecropiae,* one mutilated specimen at MCZC and four from MHNG. Of the four from MHNG, three were small and darkly pigmented, suggesting they came from an incipient colony. The fourth worker was larger and more lightly pigmented, and the mesonotal pilosity suggested *A. alfari.* This worker was designated lectotype. This collection almost certainly came from a sapling *Cecropia.* Given the prevalence of multiple colonization of saplings by queens of several species during the colony establishment phase (Longino, 1989) and the ease of obtaining mixed series when collecting from small saplings, I have not designated paralectotypes, and I have excluded all other material from the type.

*Azteca lynchi* was described from a Bolivian collection with no biological data. Gallardo (1916) placed *A. lynchi* as a subspecies of *A. alfari* with additional locality data of "Chaco boliviano." The original description and Gallardo's discussion describe sparse standing setae on the thoracic dorsum, suggesting *A. alfari* more than *A. ovaticeps.* I have put *A. lynchi* in provisional synonymy with *A. alfari.*

### MATERIAL EXAMINED

MEXICO: "Buenaventura" (Ross) [a rubber plantation on Isthmus of Tehuantepec]; *Colima:* 6 km NE Comala (Ward); *Jalisco:* 6 km NW El Tuito (Ward); *Michoacán:* 20 km S Uruapán (Ward); *Oaxaca:* 8 mi [13 km] S Valle Nacional, 2400′ [730 m] (Snelling); Hwy. 175, 3.4 mi [5.5 km] S Jacatepec, 2400′ [730 m] (Snelling); *Veracruz:* Mirador [80 km NW Veracruz] (Skwarra).

GUATEMALA: *Izabal:* Puerto Barrios (Wheeler); Quirigua (Wheeler); *Suchitepéquez:* Patulul (Wheeler).

HONDURAS: Ignacio (Mann); *Cortéz:* Choloma (Mann).

COSTA RICA: no specific locality (Tonduz); *Alajuela:* N side Volcán Arenal (Longino); *Cartago:* 4 km E Moravia (Longino); *Guanacaste:* 2 mi [3 km] E Tilarán (Janzen); 4 km W Sta. Cecilia (Longino); 6 km N Tilarán (Longino); N side Laguna Arenal (Longino); Parque Nacional Santa Rosa (Longino); *Heredia:* Finca La Selva (Janzen); 3–15 km S Pto. Viejo (Longino); *Limón:* 6 km WNW Pto. Viejo (Longino); Tortuguero (Longino); Reserva Biológica Hitoy Cerere (Longino); *Puntarenas:* San Vito de Java (Janzen); Rincón de Osa (Hogue); Sirena, Parque Nacional Corcovado (Longino); 9 km S Sta. Elena (Longino); Parque Nacional Manuel Antonio (Longino); Reserva Biológica Carara (Longino); *San José:* 1 km N Salitrales (Longino); 1 km SW Santa Marta (Longino); 2 km N Ciudad Colón (Longino); 4 km S Santa Ana (Longino); 5–7 km SW Santiago (Longino); Alto Palma (Longino).

PANAMA: no specific locality (Christophersen); *Canal Zone:* Barro Colorado Island (Zetek); Culebra (Wheeler); Corozal (Wheeler); Gatun (Wheeler); Monte Lirio (Wheeler); Red Tank (Wheeler); Rio Agua Salud (Wheeler); Summit (Krauss); *Chiriquí:* Bugaba (Champion); *Panamá:* Otoque I. (Wheeler); El Llano (Choe).

COLOMBIA: Isla Providencia (Janzen); *La Guajira:* Dibulla (Lallemand); *Magdalena:* Río Frio (Darlington); Sta. Cruz, C. Sta. Marta (Forel); 2 km ESE Minca (Longino); 5 km SE Río Frio (Longino); Cañaveral (Longino); *Tolima:* Armero (Peyton, Suarez).

VENEZUELA: no specific localty (Meinert); *Barinas:* 8–10 km WNW Sta. Barbara (Longino, Ward); 17 km SSW Ciudad Bolivia (Longino); *Miranda:* 2 km S Baruta (Longino); *Portuguesa:* San Rafael de Onoto (Longino); 3 km NNE Biscucuy (Longino); *Trujillo:* 15 km ESE Bocono (Longino); 18–19 km E Bocono (Longino); *Zulia:* El Tucoco, 45 km SW Machiques (Menke, Vincent).

TRINIDAD: no specific locality (Wheeler); no specific locality (Urich).

GUYANA: *Mazaruni-Potaro:* Kamakusa (Lang); Baracara (Wheeler); Kalacoon (Wheeler); *West Berbice:* Blairmount (Box).

SURINAME: "Paramaribo, Coppename River" (Reyne); *Paramaribo:* (Stahel).

PERU: *Madre de Dios:* Reserva Tambopata (Davidson).

BRAZIL: San Alberto (Bequaert); *Amazonas:* Flores, Manaus (Bequaert); Manaus (Huber); Manaus (Ward); *Bahia:* Bahia (=Salvador) (Ule); *Espirito Santo:* no specific locality (von Ihering); *Pará:* Pará (Göldi); *São Paulo:* São Paulo, Campo Basso (von Ihering).

BOLIVIA: *Beni:* Estación Biológica Beni, 42 km E San Borja (Ward); *La Paz:* 13 km NNE Coroico (Ward).

PARAGUAY: *Alto Paraná:* Puerto Bertoni (Strelnikou); Puerto Margarita, Río Monday (Strelnikou); *Cordillera:* San Bernardino (Fiebrig).

ARGENTINA: *Misiones:* Santa Ana (Bruch).

## *Azteca ovaticeps* Forel, 1904

Table 1

Figures 2, 3, 10–13, 22–27, 33–37, 43–47

*Azteca alfaroi* var. *ovaticeps* Forel, 1904a:44; syntype queens, workers: Brazil, Pará (Göldi) [MHNG, MCZC] (examined).

*Azteca alfari* var. *aequilata* Forel, 1904b:691; syntype workers, male: Brazil, Amazonas, Juruá Miry (ex *Cecropia* No. 5588), and Cachveira Juruá (ex *Cecropia* No. 5587), Juruá (Ule) [MHNG] NEW SYNONYMY (examined, one worker from *Cecropia* No. 5587 here designated LECTOTYPE, remainder of these two series and a third series with queens PARALECTOTYPES).

*Azteca alfari* var. *aequalis* Forel, 1906:239; syntype workers, queens, males: Brazil, Pará, Obidos (Göldi); and Brazil, Mexiana Island, Amazon delta (Hagmann) [MHNG, USNM] NEW SYNONYMY (examined, one MHNG Hagmann queen here designated LECTOTYPE, remainder of nest series PARALECTOTYPES, Göldi material excluded from type series).

*Azteca alfari* subsp. *tuberosa* Forel, 1906:240; syntype workers, queen: Brazil, Ceará (Diaz da Rocha) [MHNG, MCZC] NEW SYNONYMY (examined).

*Azteca alfari* var. *aequalis* Forel; Forel, 1908:387 (description of queen, male: Brazil, Amazon delta, Mexiana Island (Hagmann) [MHNG], examined).

### DIAGNOSIS (QUEEN)

*GTC > 10, and/or clypeus bearing a dense brush of setae;* dorsal surface of head, when viewed in profile, often with setae bridging the gap between the ocellar region and the occiput, and often with setae extending up from the clypeus almost to the ocellar region (Figs. 10–13); mesoscutum usually with even vestiture of standing setae; SI > 0.588; color variable.

## COMMENTS

I examined material of *A. aequilata* which included the two published syntype series and a third series from Juruá Miry (labeled "(Ule) 26" by Forel) which contained queens. Due to their being from the same site, and appearing nearly identical (and thus almost certainly conspecific), I have designated all three series paralectotypes to accompany the single lectotype worker. Including the third series serves to incorporate queens into the type material.

## MATERIAL EXAMINED

COSTA RICA: *Alajuela:* N side Laguna Arenal (Longino); *Guanacaste;* N side Laguna Arenal (Longino); Parque Nacional Santa Rosa (Longino); *Heredia:* Finca La Selva (Janzen); Carrillo, Parque Nacinal Braulio Carrillo (Longino); 3–15 km S Pto. Viejo (Longino); *Limón:* Zent (Wheeler); Suerre (no collector, probably Alfaro); 6 km WNW Pto. Viejo (Longino); Reserva Biológica Hitoy Cerere (Longino).

VENEZUELA: *Barinas:* 8–10 km WNW Sta. Barbara (Longino, Ward); 17 km SSW Ciudad Bolivia (Longino).

TRINIDAD: Caroni (Wheeler); no specific locality (Urich).

PERU: *Madre de Dios:* Cocha Totora (Davidson); Colpa Quebrada, nr Cocha Cashu (Davidson); Estación Biológica Cocha Cashu (Davidson); Tayacome (Davidson); Reserva Tambopata (Davidson).

BRAZIL: *Amazonas:* upper Purus (Huber); lower Purus (Huber); Cachveira Juruá (Ule); Juruá Miry (Ule); *Ceará:* Ceará (Rocha); *Pará:* Pará (Göldi, Bequaert); Pará, Obidos (Göldi); Mexiana Island (Hagmann).

BOLIVIA: *Beni:* Estación Biológica Beni, 42 km E San Borja (Ward); *La Paz:* 13 km NNE Coroico (Ward).

## VARIATION OF *A. ALFARI* AND *A. OVATICEPS*

On *A. alfari* queens, the density of setae on the dorsum of the head and on the mesoscutum increases from north to south. The setae are very sparse on specimens from Mexico in particular. The position of the posterior row of setae on the second gastric tergite varies in distance from the posterior margin, being displaced anteriorly on many South American specimens. Some queens from Mexico are light brown rather than black.

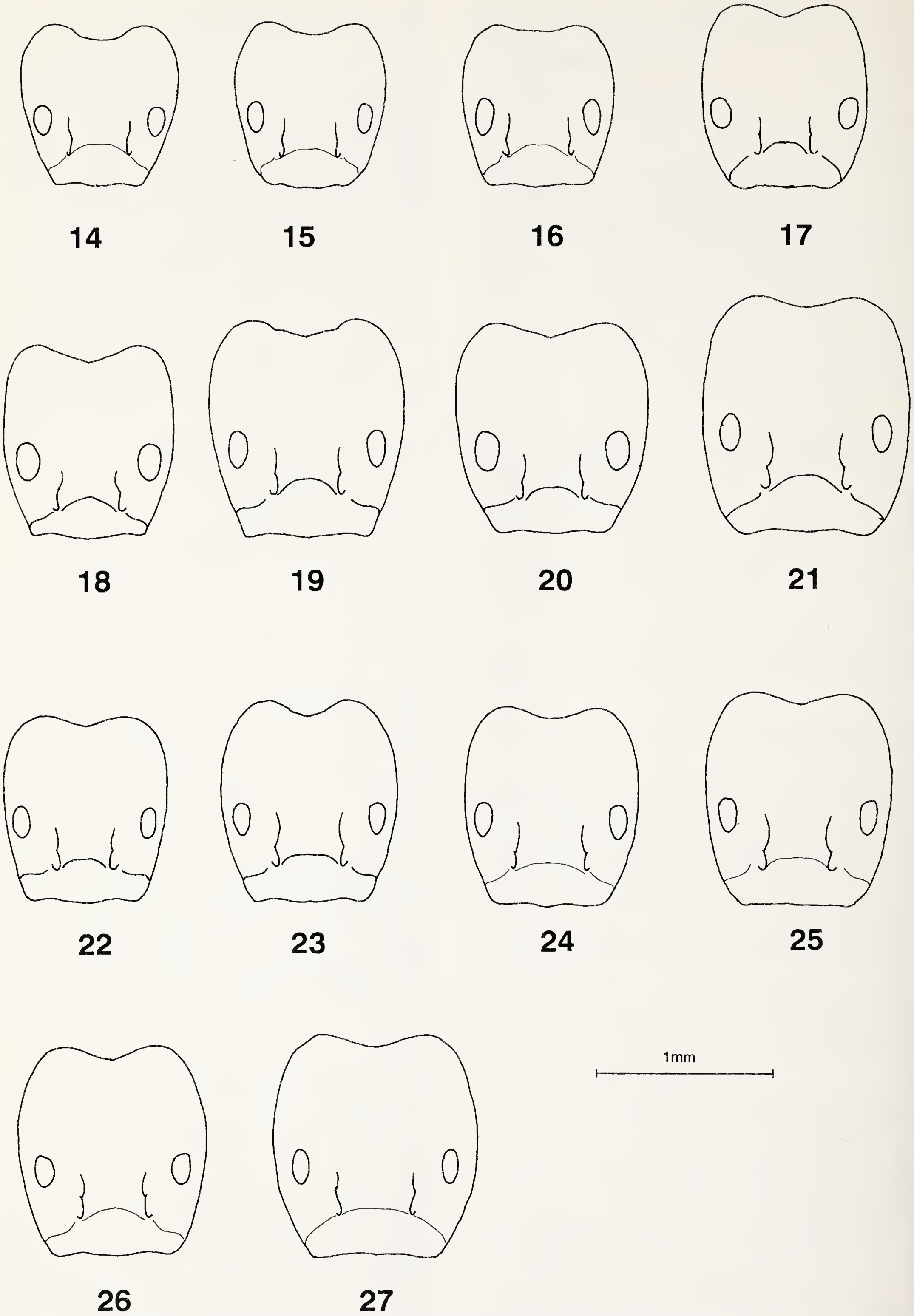
In contrast to *A. alfari,* density of setae on *A. ovaticeps* queens is highly variable and decreases from north to south. In Costa Rica, most queens have a uniform covering of an estimated 200 setae on the second gastric tergite and an even, dense vestiture of setae on the mesoscutum. Three Costa Rican queens exhibit a reduced GTC, between 10 and 40 (Fig. 1), but general abundance of setae elsewhere allies them with *A. ovaticeps.* The possibility of introgression or hybridization should be entertained. The head, in profile, usually exhibits abundant setae on the occiput, which spreads down the front bridging the gap between the occiput and the setae of the ocellar region.

In South American *A. ovaticeps,* general body pilosity is always less than the Costa Rican material, is highly variable, and can approach the state of *A. alfari.* GTC is always very reduced compared to Costa Rican material but is still usually 10 or more, distinguishing *A. ovaticeps* from *A. alfari.* Setae on the second gastric tergite are usually somewhat symmetrically arranged on the dorsal surface of the abdomen. The head, in profile, may or may not have setae bridging the gap between the occiput and the ocellar region.

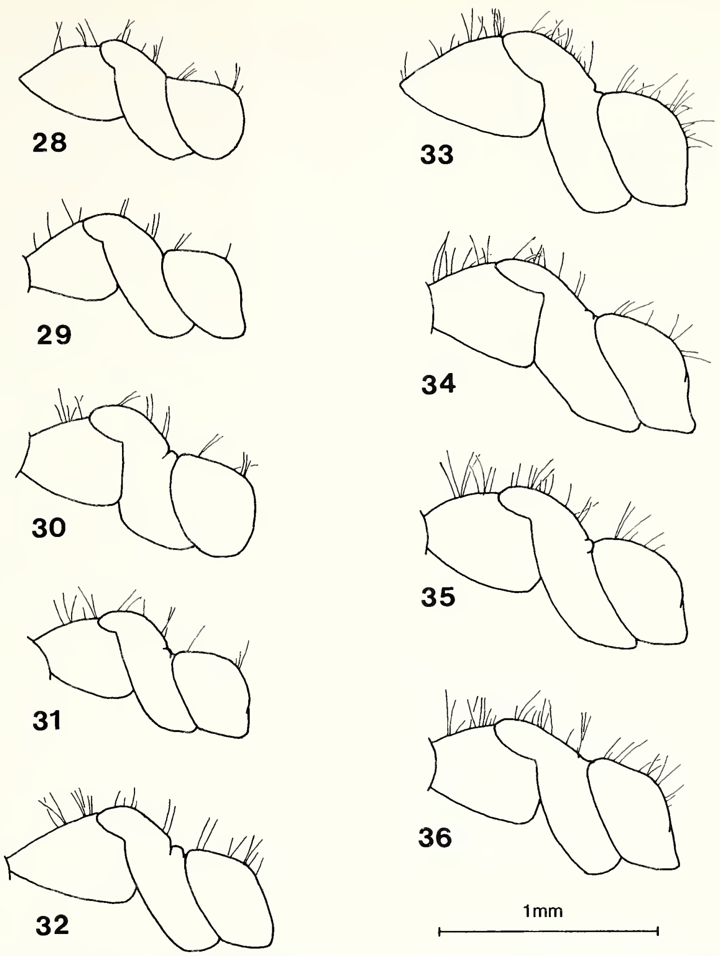
The most reliable *A. ovaticeps* character throughout South America is a dense brush of setae on the clypeus, and the cuticle is always light brown beneath the brush, even if the rest of the body is black. To appreciate this character, it is best to have comparative material of *A. alfari.* Material of *A. alfari* and *A. ovaticeps* from two sites in Bolivia (Ward collection) was the most difficult to separate. Body color (black) and overall pilosity were very similar. GTC for four *A. alfari* queens was 0, 0, 0, and 3, whereas for three *A. ovaticeps* queens it was 2, 9, and 11. However, the seven queens clearly differed in the presence or absence of a clypeal brush.

Workers of *A. alfari* and *A. ovaticeps* are not always distinguishable. Earlier taxonomy of the *A. alfari* group relied heavily on worker head shape, a character which shows nearly continuous variation and is rarely used in this revision (Figs. 14–27). There is a tendency for *A. alfari* workers to have more triangular heads (Figs. 14, 18–20), but the significance of this needs to be evaluated in the context of allometric shape change related to worker size.

The two species are most distinguishable by degree of pilosity, particularly on the mesonotum (Figs. 28–36). When multiple samples are available from a locality where both species occur, they are usually easily separable into *A. alfari* and *A. ovaticeps.* The former have a "clean" look, with relatively few, long setae of somewhat regular length, whereas the latter have a "scruffy" look, with many setae of irregular lengths. Geographic variation obscures this difference when examining single collections from scattered localities. MSC values for the *A. alfari* group as a whole (Fig. 37) exhibit a pronounced bimodal distribution, but there is a zone of overlap between the two species. Species determinations for the zone of overlap in Figure 37 were made by association of workers with sexuals, or by "gestalt"



**Figures 14–27.** *Azteca alfari* group workers, frontal view of head. Top 2 rows are *A. alfari*; bottom 2 rows are *A. ovaticeps*. **14.** Costa Rica (*A. alfari* lectotype). **15.** Mexico (*A. fumaticeps* syntype). **16.** Brazil (*A. cecropiae* lectotype). **17.** Paraguay (*A. mixta* paralectotype). **18.** Argentina (*A. argentina* syntype). **19.** Costa Rica. **20.** Venezuela. **21.** Mexico. **22.** Venezuela. **23.** Peru. **24.** Brazil (*A. tuberosa* syntype). **25.** Brazil (*A. aequilata* lectotype). **26.** Brazil (*A. ovaticeps* syntype). **27.** Costa Rica.



**Figures 28–36.** *Azteca alfari* group workers, lateral view of mesosoma. Setal patterns were drawn, as for queen head profiles, by focusing on the midline. Left-hand column is *A. alfari*; right-hand column is *A. ovaticeps*. **28.** Mexico (*A. fumaticeps* syntype). **29.** Costa Rica (*A. alfari* lectotype). **30.** Panama. **31.** Brazil (*A. cecropiae* lectotype). **32.** Paraguay (*A. mixta* paralectotype). **33.** Costa Rica. **34.** Brazil (*A. aequilata* lectotype). **35.** Brazil (*A. ovaticeps* syntype). **36.** Brazil (*A. tuberosa* syntype).

developed from multiple samples from one locality. Some of the overlap is probably due to loss of setae on older specimens of *A. ovaticeps*.

Figures 38–46 illustrate male antennae across the geographic range of *A. alfari* and *A. ovaticeps*. From Costa Rica to Paraguay, *A. alfari* exhibits a highly asymmetrical third antennal segment, with a pronounced distal lobe (Figs. 39–42). There is variation in the degree of development of the asymmetry. Figure 40 shows the most extreme reduction of the lobe observed in six separate collections of males from Venezuela. In contrast, *A. ovaticeps* males exhibit a much more cylindrical third segment (Figs. 43–46). In South America there is almost no trace of asymmetry, the segment being very cylindrical (Figs. 44–46). In Costa Rica the third segment is more swollen and exhibits greater asymmetry (Fig. 43), but Costa Rican *A. alfari* exhibit the greatest asymmetry observed (Fig. 39) and are distinct from

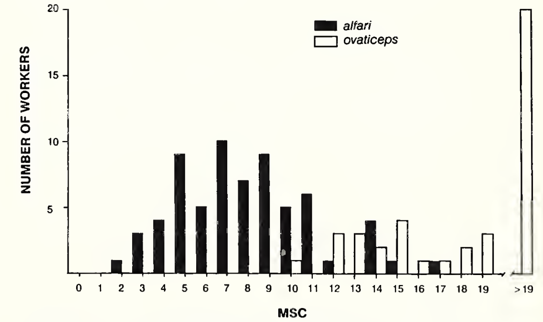
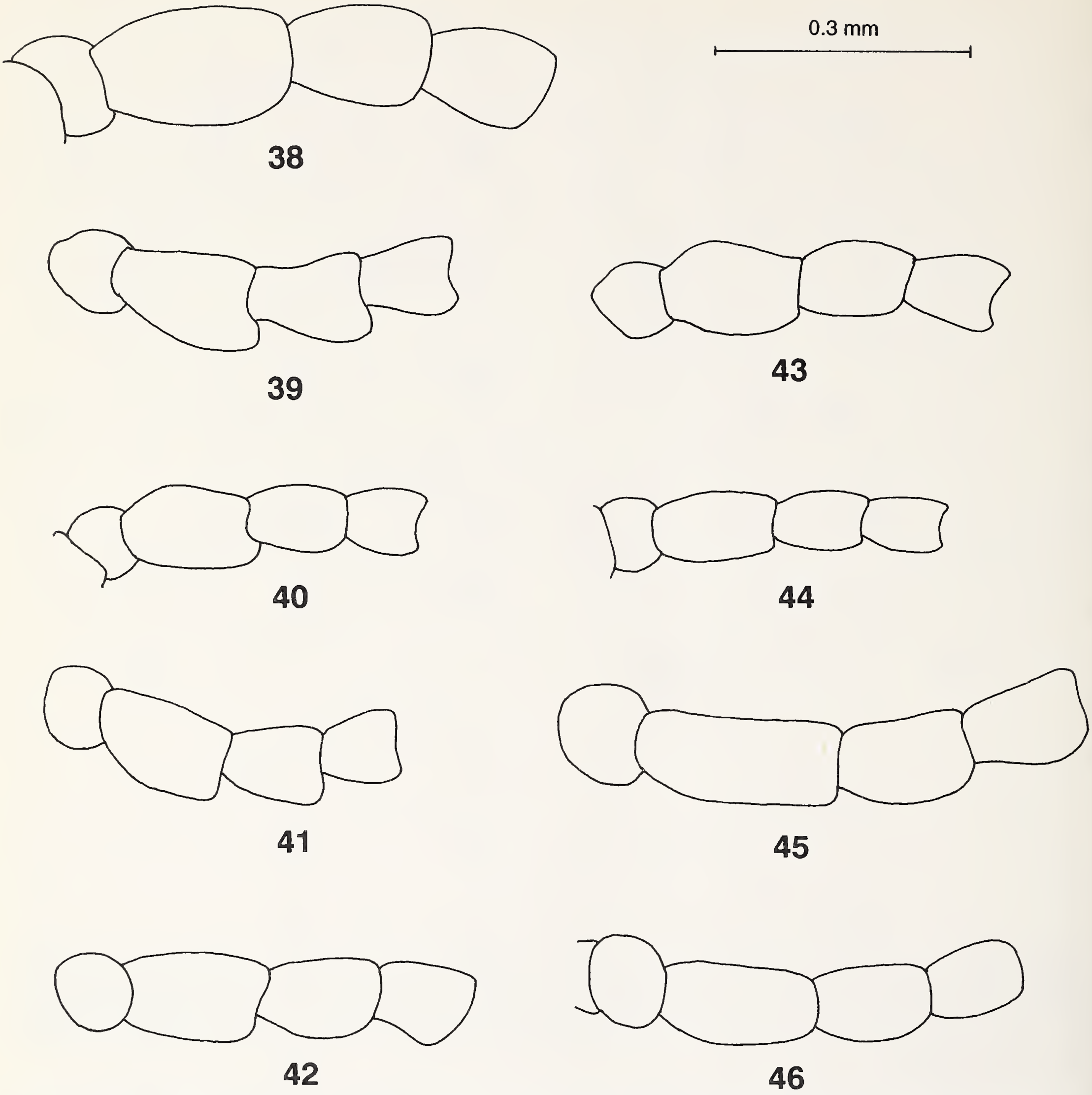


**Figure 37.** Distribution of MSC values (number of mesonotal setae on workers) for *Azteca alfari* and *A. ovaticeps*. Seven of the *A. ovaticeps* specimens with MSC < 20 were old, collected before 1910, and have probably experienced seta loss through wear.



**Figures 38–46.** Male antennae, segments 2–4. Antennae are oriented to show maximum width of segment 3. Silhouettes are drawn without the dense fringe of setae. *Azteca alfari:* **38,** Mexico; **39,** Costa Rica; **40,** Venezuela; **41,** Trinidad (*A. lucidula* paralectotype); **42,** Paraguay (*A. mixta* paralectotype). *Azteca ovaticeps:* **43,** Costa Rica; **44,** Venezuela; **45,** Brazil (*A. aequilata* paralectotype); **46,** Brazil (*A. aequalis* paralectotype).

Costa Rican *A. ovaticeps.* Specimens from southwestern Mexico are the most aberrant (Fig. 38), with male segment 3 resembling neither *A. alfari* nor *A. ovaticeps* from further south. Queen and worker characters are very like *A. alfari,* however, and these collections are provisionally identified as *A. alfari* until the nature of character change from Mexico to Costa Rica is better known.

## NATURAL HISTORY OF THE *A. ALFARI* GROUP

The two *A. alfari* group species are obligate *Cecropia* inhabitants. Wheeler (1942) referred to *A. alfari* (sensu lato) as the "Cecropia ant *par excellence.*" All collections described in the literature or examined by me were either collected from *Cecropia* or lack biological data. Types of *A. alfari* were from *Cecropia* trees on the Atlantic slope of Costa Rica. The lectotype of *A. cecropiae* was collected "from a *Cecropia,*" and the von Ihering collections from near São Paulo were "from swamp *Cecropia.*" The paralectotype series of *A. mixta* was from Fiebrig's (1909) study of *Cecropia* in Paraguay. Syntypes of *A. fumaticeps* were from Ross's (1909) study of *Cecropia* in Mexico. Syntypes of *A. breviscapa, A. langi,* and *A. zonalis* were from *Cecropia.* Syntypes of *A. aequilata* were collected by Ule from *Cecropia* trees along the Juruá in Brazil.

This species group is nearly coextensive with *Ce-*

*cropia* trees, except at high elevations and on islands where *Cecropia* has colonized without ants (Janzen, 1973). It occurs from southern Mexico to Paraguay and northern Argentina, and on several Caribbean islands. It is generalized in its use of *Cecropia* species, even within microhabitats. I have observed colonies of *A. alfari* inhabiting *C. obtusifolia* Bertoloni, *C. peltata* L. and *C. insignis* Liebmann in Costa Rica, and *C. peltata, C. palmatisecta* Cuatrecasas, and *C. libradensis* Cuatrecasas in Venezuela. I have collected *A. ovaticeps* from *C. obtusifolia, C. peltata,* and *C. insignis* in Costa Rica and from *C. peltata* in Venezuela.

The *A. alfari* group as a whole is found in more disturbed habitats than other obligate *Cecropia* inhabitants such as *A. muelleri, A. constructor,* and *A. xanthochroa* (Benson, 1985; Longino, unpubl. obs.). The two species within the *A. alfari* group, although frequently occurring in adjacent trees, may also exhibit slightly different habitat preferences with respect to each other. *A. alfari* sensu stricto is found in habitats at the high end of the disturbance spectrum. In Costa Rica, *A. alfari* is the most frequently encountered species in *Cecropia* trees along roadsides and pasture edges, in areas that are far from forest or forest patches. It also occurs in and around forest patches, but there it occurs at a lower frequency, sharing *Cecropia* populations with several other *Azteca* species (Longino, 1989). *Azteca alfari* also exhibits a wide geographical range, occurring at the tropical/subtropical transitions in Mexico and Paraguay. This species' presence at the geographical and climatic limits of the ant–*Cecropia* association may be related to its affinities for disturbed, open habitats in the center of its range.

In contrast, *A. ovaticeps* seems to be associated more with wet forest habitat or, at least, forest edge, and its geographic range is smaller and more centrally located. Although perhaps associated with disturbance in the form of treefall gaps or shifting river edges, it does not seem to thrive in areas of continual anthropogenic disturbance. At the La Selva biological station in Costa Rica it is the most common *A. alfari* group species, whereas at other sites farther from intact forest *A. alfari* sensu stricto is more abundant. Judging from old collections, *A. ovaticeps* was very common along river margins in the Amazon basin. With increasing human disturbance, *A. alfari* may be much more common in this area than it used to be. Davidson has made dozens of collections of ants from *Cecropia* trees at and around Cocha Cashu Biological Station in Manu National Park, Peru, an extremely remote area with almost no human disturbance; all have been *A. ovaticeps.* In contrast, her collections from the nearby Tambopata reserve, a site with somewhat more disturbance, contain an *A. alfari* queen in addition to many *A. ovaticeps* queens.

A long-standing debate revolves around whether the ant–*Cecropia* association is a mutualism (reviewed in Bailey, 1922; and Janzen, 1969). Recent studies suggest that the *A. alfari* group may be less effective than other *Azteca* species in defending *Cecropia* trees from herbivores (Andrade and Carauta, 1982; Andrade, 1984). In Costa Rica, *A. alfari* group species are slow to respond to mechanical disturbance of their nest trees, and their nest trees suffer increased herbivory and reduced growth relative to trees inhabited by other obligate *Cecropia* ants (Longino, unpubl. obs.).

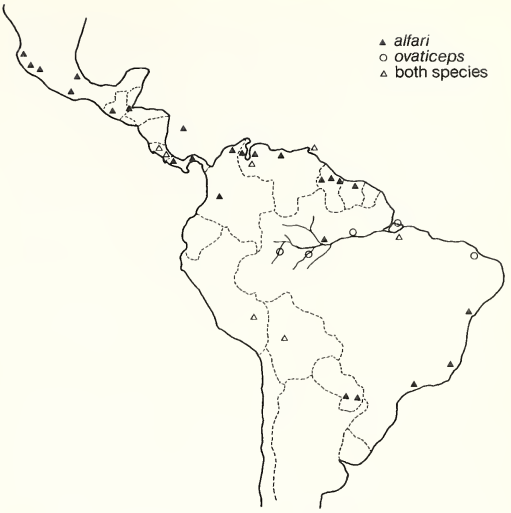


**Figure 47.** Distribution of *A. alfari* and *A. ovaticeps.*

## SPECIES EXCLUDED FROM THE *A. ALFARI* GROUP

### *Azteca lucida* Forel NEW STATUS

*Azteca alfaroi* race *lucida* Forel, 1899:113; syntype workers: Guatemala, Pantaleon, 1700′ (Champion) [MHNG] (examined).

The syntype workers have standing hairs on the tibae, and the major workers have large, subquadrate, nearly glabrous heads, completely unlike the heads of major workers in the *A. alfari* group. In the description, Forel states that *A. lucida* was collected from *Cecropia,* but the labels I observed on the syntypes contain no biological data. The syntypes may or may not have been collected from a *Cecropia,* but there is no evidence that this species is an obligate inhabitant.

## DISCUSSION

Recent taxonomic studies of ants are revealing the frequent occurrence of broadly sympatric sibling species (*e.g.* Trager, 1984; Ward, 1985). Some may view this as a simple swing of the pendulum from lumpers to splitters, but this form of splitting is fundamentally different from that of Forel, Wheeler, and others. The uncontrolled proliferation of names occurring in the early part of this century was largely based on geographic variation with no critical evaluation of character variation within or between regions. Current studies frequently split within regions and lump across regions, the opposite of past practice. Recent discoveries in ant taxonomy have, in part, been due to an increased abundance and availability of museum material. But a more important factor has been the thorough examination of local ant communities. Knowledge of sympatric ant communities gives the first clue to the presence of sibling species, because subtle species differences within a site are not masked by geographic variation.

In this paper, ecological evidence of microsympatric discrete morphologies has been used to justify the delineation of two species. The differences between the two species can be very subtle, and I might not consider them an adequate basis for species distinction were it not for the ecological evidence. The primary differences at any one site are degrees of pilosity, but the details of seta abundance and distribution are highly variable geographically.

Many taxonomists have a biological species concept in mind when describing species. Members of a species are presumed to be united by potential or actual gene flow. When lineage concepts are added, members of a species are presumed to share ancestry unique to them. Thus, a first hypothesis in this study is that *A. alfari* and *A. ovaticeps* satisfy these conditions, being two reproductively isolated lineages, each with its own unique ancestor and each reproductively continuous throughout its range. However, the two "species" as defined here are in reality two phenetic clouds of correlated characters of museum specimens and should not automatically be assumed to be two monophyletic lineages. The following alternatives could complicate the story and should be evaluated in future studies of the *A. alfari* group.

Either or both species could be composed of numerous sibling species, their distributions being allopatric, parapatric, or largely parapatric with narrow zones of sympatry. The geographic variation observed could thus be due to species differences. Within *A. alfari,* there are morphological gaps among material from Mexico (*e.g. A. fumaticeps*), Central America (*e.g. A. alfari* sensu stricto), northern South America and Amazonia (*e.g. A. virens, A. cecropiae*), and southern South America (*e.g. A. mixta*). Within *A. ovaticeps,* there are fairly striking differences among material from Costa Rica, Venezuela, Amazonia, Peru, and Bolivia. These geographic gaps in morphology are accompanied by gaps in material examined, however; and the nature of character change in those gaps remains unknown.

The possibility of multiple sibling species raises an additional hypothesis: that one of the "species" defined here is paraphyletic with respect to the other. For example, one sibling species of the *A. alfari* lineage could have split, giving rise to a contemporary sibling species within *A. alfari* and the lineage that became *A. ovaticeps.* An even more intriguing possibility, although distressing to a taxonomist, is that one of the species is polyphyletic. For example, there could be selection favoring increased pilosity in some habitats, where *A. alfari* group queens are in frequent contact with competing species of *Azteca* (*A. muelleri, A. constructor,* and *A. xanthochroa*). There could be conditions scattered throughout the range of the widespread *A. alfari* lineage that favor the existence of a genetically isolated *A. ovaticeps*-like form. *Azteca ovaticeps* as defined here could have arisen numerous times independently, as distinct lineages descended from ancestral *A. alfari*-like populations.

With this much uncertainty regarding the status of the *A. alfari* group species, is this taxonomic treatment of the group justified? I think there are several reasons for the approach taken here. First, this study alerts investigators to the presence of sympatric species within the *A. alfari* group. Second, when two species are present, names are available for use in ecological and evolutionary studies. An investigator in Manaus, on reading an ecological study on *A. ovaticeps* and *A. alfari* in Costa Rica, will be able to make direct comparisons with the cognate species pair found locally. If new studies reveal multiple species within the current species boundaries, identities of the former *A. alfari* and *A. ovaticeps* can be established region by region, and a continuity can be maintained among literature using old and new nomenclature. Retaining the original nomenclature (prior to this study) has obvious drawbacks. Using the single name *A. alfari* for all *A. alfari* group members obscures the presence of sympatric species; using the multitude of infraspecific names not only obscures the presence of sympatric species but hinders comparability from region to region.

Hillis (1988) recognized three phases in the development of a taxonomic species concept, using the anuran *Rana pipiens* complex as an example. He termed these phases the "thesis of typological species, the reaction to typology or antithesis of polytypic species, and the synthesis of evolutionary species." For many groups of neotropical ants, taxonomy has stalled in phase one. A phase two approach has been taken in this report. I suspect that as additional material is obtained and molecular techniques provide additional characters, zones of sympatry will be found and a number of evolutionary species will emerge from each of my polytypic species.

Further understanding of the *A. alfari* group will require additional collections from mature colonies. I hope this study stimulates further collection throughout the range of the *A. alfari* group and encourages the collection of voucher material in ecological studies of the *Azteca–Cecropia* association.

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## The Net-Winged Midge Fauna (Diptera: Blephariceridae) of Antioquia Department, Colombia

Charles L. Hogue and Inés Bedoya Ortiz

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# THE NET-WINGED MIDGE FAUNA (DIPTERA: BLEPHARICERIDAE) OF ANTIOQUIA DEPARTMENT, COLOMBIA

CHARLES L. HOGUE[1] AND INÉS BEDOYA ORTIZ[2]

**ABSTRACT.** The "net-winged midge" fauna of Antioquia Department, Colombia, was studied and found to consist of 14 species in the genera *Paltostoma* and *Limonicola* (Blephariceridae, Apistomyiini). Of these, ten are described as new: *P. roldani* Hogue and Bedoya, *P. aspergonympha* Hogue, *P. charadrae* Hogue, *P. eldorado* Hogue, *P. inca* Hogue, *P. andeana* Hogue and Bedoya, *L. lichanos* Hogue and Bedoya, *L. astylis* Hogue, *L. medius* Hogue, and *L. kolomeros* Hogue. *Paltostoma saltana* Edwards, 1929, and *L. davila* Hogue, 1982, plus two unidentified *Limonicola,* known only from larvae, comprise the remainder. Keys to species and general ecological notes are also provided.

**RESUMEN.** Se estudió la fauna de "mosquitas de alas reticuladas" del Departamento de Antioquia, Colombia. Esta consta de 14 especies de los géneros *Paltostoma* y *Limonicola* (Blephariceridae, Apistomyiini). De estas, diez son descritas como nuevas especies: *P. roldani* Hogue & Bedoya, *P. aspergonympha* Hogue, *P. charadrae* Hogue, *P. eldorado* Hogue, *P. inca* Hogue, *P. andeana* Hogue & Bedoya, *L. lichanos* Hogue & Bedoya, *L. astylis* Hogue, *L. medius* Hogue, y *L. kolomeros* Hogue. Las restantes son *P. saltana* Edwards, 1929 y *L. davila* Hogue, 1982, mas dos larvas de *Limonicola* no identificadas. Se incluyen claves de las especies y notas ecológicas generales.

## INTRODUCTION

The net-winged midges, or Blephariceridae, are an ancient and highly specialized family of nematocerous flies adapted to torrential waters, about whose neotropical components exists only a meager body of literature (Hogue, 1977, 1981a, 1982a). Indications from unpublished regional investigations by Hogue are that many undescribed species exist in the region and that possibly the richest fauna of any country is to be found in Colombia. We have discovered many new species in the Department of Antioquia during our joint field studies there. Also, detailed ecological data have been obtained regarding these species, primarily by Bedoya for her matriculation in biology at the Universidad de Antioquia (Bedoya, 1984). The purpose of this paper is to describe the fauna and summarize the other information now available from the area.

The Department of Antioquia is situated in the northwestern portion of Colombia and is one of the larger political divisions of the country, with a land area of 63,612 square kilometers. Its topography and climate are diverse, the former including extensive mountainous terrain (corresponding to the northern extremes of the Andean Cordilleras Central and Occidental), where swift, rocky streams abound. A long rainy season of approximately seven months occurs in the period April to November, providing the constant ground water that supplies numerous permanent flows. Details of the aquatic habitats of Antioquia and locations of some of the collecting sites are presented by Roldán (1988:1–5) and Bedoya and Roldán (1984). Bedoya and Roldán also give physicochemical data on many of the streams from which blephariceridis were taken (see summary under Notes on Ecology).

The authors made numerous collecting trips to several portions of the Department from 1982 to 1986, when the material for this study was gathered.

## METHODS

### PREPARATION OF MATERIAL

Routinely it has been found useful to dissect apart the elements of the male terminalia (keeping one or two specimens intact) and mount them on a microscope slide as follows: first, the outer gonostylus is severed at its base and positioned with the medial surface up. Then, the cerci with accompanying inner arms are freed by breaking the epandrial membrane at the base of the former; this complex is removed and placed on the slide dorsal side up. Finally, the mesosomal complex (gonites, tines, aedeagus, and associated structures) is dislocated from the genital capsule by severing the articulations of the dorsal gonite arm and condyle on the margin of the genital capsule, and lifting it out. It is also oriented on the slide with its dorsal side up.

### MORPHOLOGICAL TERMINOLOGY

The terminology for the descriptions that follow is mostly that established in Hogue's earlier treatments of blepharicerid anatomy (1978, 1979, 1981b, 1987). For the con-

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[1] Present address: Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, USA.

[2] Capitania de Puerto, Providencia Isla, Colombia.

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venience of users of this paper, key structures are labeled in figures here for the male terminalia (Figs. 5–8), female terminalia (Fig. 13), pupa (Fig. 20), larva (Fig. 56), adult heads (Figs. 58, 59), and tarsi (Fig. 61). A glossary is provided for the various forms taken by the modified (generally short, peglike) dorsal sensilla of the larvae (Fig. 126). Both primary and secondary sensilla often modify and multiply with succeeding instars ("neotrichy"), their numbers obscuring the identification of the primary setae in many cases. The peglike setae are often well developed and, on intermediate abdominal segments, form two linear series—one beginning in the antero-mediodorsal position, extending laterad along the anterolateral margin of the segment and curving sharply ventrad to the base of the pseudopod, and a second complementary series following a similar path on the posterior portion of the segment. We call the combined set the "circumlateral series" (Fig. 56) ("marginal armature" of Dumbleton, 1963), comprised of an "anterior portion" and "posterior portion." The series is characteristic of many larvae of the Apistomyiini, particularly *Paltostoma,* in Antioquia. The setae arise from and follow corresponding elevated ridges—the "circumlateral ridges."

We use the established term "*pollex*" (Lat. thumb) for the ventrobasal area of tarsomere 5, which is set with a group of heavy oversized setae. Whereas they do not arise from a distinct convexity, the function of these setae is the same as the thumblike projection of many grasping insect tarsi, especially among ectoparasites, namely to provide a catch or opposing member for the claw(s) closing upon it. Blephariccerids use the apparatus for clinging tenaciously together during mating and to perches. Hogue erroneously referred to this organ as the "calcipala" in an earlier work (1982).

In keeping with common usage by students of the family, the conspicuous lobes of the 10th tergite in the male terminalia are called "cerci," even though their homology with these elements in other Diptera is not demonstrated.

In the Apistomyiini, the ventromedial area of the VIIIth abdominal segment of the female is modified into a distinct, bilobed structure, which becomes a part of the terminalia and to which we refer here simply as "sternite VIII."

In general form, apistomyiine larvae may be "lobiform" or "denisciform." In the former (e.g., Fig. 101), the anterior and posterior margins of the abdominal segments are smoothly rounded, with a wide space between the lateral lobes whether or not the larva is contracted. In the latter condition (e.g., Fig. 56), the anterior and posterior margins of the abdominal segments are angular and in contact when the larva is contracted.

We express numbers of setae in groups in general terms ("few" = 3–5, "several" = 6–12, "numerous" = 13–30, "very numerous" = 31–70), followed by actual counts if determinable and appropriate.

All measurements are given in millimeters. The formula for comparative sizes of male vs. female pupae is (L)(W) male/(L)(W) female. Leg segment proportions are "progressive," i.e., beginning basally, the relative length of each segment compared to its next more basal neighbor. Larval body length is taken from fully mature specimens (usually prepupal larvae, i.e., those showing only a trace of the pupal branchiae).

## STAGE ASSOCIATIONS

Stage associations were made by careful application of the variously reliable methods, some of which were used by Hogue elsewhere (Hogue, 1973). These are as follows:

1. Ontogenetic method (called "continuity method" in Hogue, 1973): This matches larva–pupa, pupa–adult, by inspection of the pharate phase of the later stage within the earlier. The later stage may be seen through the integument of the earlier in the intact specimen, dissected out of the earlier, or collected with the exuviae at the time of ecdysis. This is a very reliable method. Errors sometimes occur when structures on the new insect are not clearly discernible through the body wall of the old.
2. Statistical method: When more than one species is present at a specific site, the different stages are equated on the basis of their similar frequency of occurrence. This is often unreliable and sometimes misleading, because at certain times in the development of a population one stage predominates in numbers and earlier stages decrease as later stages increase.
3. Syntopic method: This associates stages merely upon their common occurrence at a single collection site, when no other species are present. This is a moderately reliable procedure, but there always is the possibility that additional species are present.
4. Proximity method: This is for immatures only and assumes conspecificity of these stages found in immediate proximity (tightly grouped) in a microhabitat or portion thereof. Fairly reliable, this method requires care during collecting to isolate material taken in contiguity.
5. Phyletic inference method: The early stages are associated on the basis of structural similarity to known stages of related species. It is frequently unreliable because of convergence and character inconsistency.
6. Individual rearing: Individual specimens are reared in isolation. It is an absolutely reliable method but difficult to manage for larva–pupa without special laboratory equipment to maintain specimens alive in oxygenated water. Adults sometimes will emerge from pupae carefully collected and placed on a damp substrate. No individual rearings were made for this study.

## NOMENCLATURE

We chose to base new species primarily on adult males because they are the most consistently distinctive stage. Also, when names descriptive of anatomy are applied to this stage the possibility is avoided of producing inappropriate names if stage associations have to be changed.

Authorship of some of the new species is attributed only to Hogue (see Classification). These were discovered by him from material collected outside of and subsequent to Bedoya's project (Bedoya, 1984).

## MATERIAL

A total of 3,666 specimens were available for this work. They were collected, along with environmental data, from the Department of Antioquia in northwestern Colombia. All the material is retained in the collection of the Entomology Section of the Los Angeles County Museum of Natural History (indicated by "LACM" where the material is listed under Specimens Examined); a few were borrowed from the American Museum of Natural History in New York ("AMNH").

The study has suffered somewhat from a lack of adequate material for several of the rarer species. We urge stream biologists working in Colombia to collect blephariccerids at every opportunity, making sure to take large series of the stages available and look thoroughly for free-flying adults.

# BLEPHARICERIDAE OF ANTIOQUIA DEPARTMENT

## CLASSIFICATION

The blephariceríd fauna of Antioquia Department, Colombia, consists of the following taxa:

*Paltostoma* Schiner
1. *Paltostoma roldani* Hogue and Bedoya, n. sp.
2. *Paltostoma aspergonympha* Hogue, n. sp.
3. *Paltostoma charadrae* Hogue, n. sp.
4. *Paltostoma eldorado* Hogue, n. sp.
5. ? *Paltostoma saltana* Edwards, 1929
6. *Paltostoma inca* Hogue, n. sp.

*Paltostoma schineri* group
7. *Paltostoma andeana* Hogue and Bedoya, n. sp.

*Limonicola* Lutz
8. *Limonicola lichanos* Hogue and Bedoya, n. sp.
9. *Limonicola astylis* Hogue, n. sp.
10. *Limonicola davila* Hogue, 1982
11. *Limonicola medius* Hogue, n. sp.
12. *Limonicola kolomeros* Hogue, n. sp.
13. *Limonicola* unidentified larva 1
14. *Limonicola* unidentified larva 2

## KEYS TO THE BLEPHARICERIDAE OF ANTIOQUIA DEPARTMENT

### Adults

General features of the adults are sometimes difficult to determine on dried specimens. They may be more clearly seen in alcoholic material in which deformations have not occurred. Definitive species identification is best done with the terminalia; in the male, the shape of the outer gonostylus is the most useful character and is often visible even in dried or alcoholic specimens. Slide mounts are necessary to reveal internal characters of the terminalia, setal patterns of the thorax, and mouthparts, as well as external details of the tarsi, etc.

*Adult males (*Paltostoma saltana *inadequately known)*

1. *General.*—Mouthparts well developed, proboscis usually longer than head width (Fig. 1). Apex of hind tibia and basitarsus never inflated (Fig. 4). Anal lobe of wing usually small or completely undeveloped. *Terminalia.*—Sperm sac small (width never greater than 0.75 length of aedeagal rods), walls of aedeagal rods thin, internal canal not evident (Fig. 6). Lateral tine present or absent, if latter often replaced by a ventral plate. Inner gonostylus entirely distinct from aedeagal guide (Fig. 5). Inner arm of cercus long and well sclerotized, apex approximate to contiguous with opposite member (Fig. 8). .................... *Paltostoma* ... 2
   *General.*—Mouthparts poorly developed, proboscis much shorter than head width (Fig. 84). Apex of hind tibia and tarsal segments 1–3 often inflated (Fig. 109). Anal lobe of wing often produced. *Terminalia.*—Sperm sac large (approximately as wide or wider than length of aedeagal rods), walls of aedeagal rods thick, internal canal evident (Fig. 89). Lateral tine completely absent. Inner gonostylus fused to aedeagal guide (Fig. 88). Inner arm of cercus short and poorly sclerotized, apex distant from opposite member (Fig. 91). .................... *Limonicola* ... 7
2. *General.*—Palpus 1-segmented. *Terminalia.*—Lateral tine present. .................... 3
   *General.*—Palpus 2-segmented. *Terminalia.*—Lateral tine absent. .................... 6
3. *General.*—Fore tarsus unlike mid and hind tarsi (Fig. 30): longer and stouter; fore tarsomere 5 straight and expanded distad, without pollex; mid and hind tarsomeres 5 similar, curved, with pollex of heavy setae; fore claws simple, mid and hind claws sickle-shaped, with sub-basal tooth. *Terminalia.*—Sperm sac and bases of aedeagal rods with spiculae on inner walls (Fig. 10). .................. *P. aspergonympha*
   *General.*—Tarsi similar on all legs (Fig. 3): tarsomeres 5 curved, with basiventral pollex of heavy setae; claws all sickle-shaped, with subbasal tooth. *Terminalia.*—Sperm sac and aedeagal rods without internal armature. ... 4
4. *General.*—Ultimate antennal segment longer than penultimate (Fig. 1). *Terminalia.*—Lateral tine spined at base. .................... 5
   *General.*—Ultimate antennal segment shorter than penultimate (Fig. 33). *Terminalia.*—Lateral tine unarmed. .......... *P. charadrae*
5. *General.*—No characters. *Terminalia.*—Outer gonostylus simple, ovoid in outline. Outer aedeagal rods arising directly from posterolateral corners of sperm sac (Fig. 42). . *P. eldorado*
   *General.*—No characters. *Terminalia.*—Apex of outer gonostylus angled sharply ventrad (Fig. 7). Outer aedeagal rods arising more or less laterally from sperm sac, bases gently arching (Fig. 6). ...................... *P. roldani*
6. *General.*—Proboscis long (2.4–2.6 width of head). Length of basal palpal segment 2.0 distal. *Terminalia.*—Outer gonostylus with conspicuous ventral tooth on ventral margin (Fig. 68). Inner gonostylus very short and with acute apex (Fig. 66). ................ *P. andeana*
   *General.*—Proboscis very long (3.0 head width). Length of basal palpal segment 1.5 distal. *Terminalia.*—Outer gonostylus entire (Fig. 64). Inner gonostylus long and with rounded apex (Fig. 62). ........................ *P. inca*
7. *General.*—Ultimate segment of antenna elongate, flask-shaped (Fig. 102). *Terminalia.*—Inner gonostylus very small, mostly fused with aedeagal guide (Fig. 92). .......... *L. astylis*
   *General.*—Ultimate segment of antenna cylindrical, subequal to penultimate (usually slightly

smaller). *Terminalia.*—Inner gonostylus with well-developed apex, free of aedeagal guide. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

8. *General.*—First (and sometimes second) flagellar segment of antenna reduced, smaller and more condensed than others (Fig. 112). *Terminalia.*—Inner gonostylus bifurcate, sublobes broadly rounded apically (Fig. 118). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *L. kolomeros*
   *General.*—Flagellomeres of antenna equal in size and shape throughout (except terminal which may be longer than rest). *Terminalia.*—Inner gonostylus simple. . . . . . . . . . . . . . . 9
9. *General.*—Hind tarsomeres of same diameter as tibia (not inflated) (Fig. 86). *Terminalia.*—Outer gonostylus very much elongated, straplike, its ventral margin at base not lobulate (Fig. 90). . . . . . . . . . . . . . . . . . . . . . . . . *L. lichanos*
   *General.*—Hind tarsomeres inflated (Fig. 109). *Terminalia.*—Outer gonostylus elongate but not greatly so, its ventrobasal margin lobulate (Fig. 116). . . . . . . . . . . . . . . . . . . . . . . . . . . 10
10. *General.*—No characters. *Terminalia.*—Ventrobasal lobe of outer gonostylus short, less than half the length of gonostylus (making entire organ L-shaped) (Fig. 116). Apex of inner gonostylus only slightly narrrowed, more or less straight, base only a little broader than apex (Fig. 114). . . . . . . . . . . . . . . . . . . . . *L. medius*
   *General.*—No characters. *Terminalia.*—Ventrobasal lobe of outer gonostylus long, about same length as gonostylus (making entire organ V-shaped). Apex of inner gonostylus constricted and angled outward, base broad. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *L. davila*

*Adult females (*Paltostoma saltana *and* Limonicola kolomeros *unknown)*

1. *General.*—Mouthparts well developed or not, but labellar lobes always much shorter (or only slightly longer) than remainder of labium; mandibles present or not. *Terminalia.*—Spermathecae oblong (Fig. 15) or spherical (Fig. 71). Medial depression of sternite VIII simple, without a "collarlike" subdivision (Fig. 70). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Paltostoma* . . . 2
   *General.*—Mouthparts always poorly developed, labellar lobes much longer than remainder of labium; mandibles never present. *Terminalia.*—Spermathecae pear-shaped (Fig. 73). Medial depression of sternite VIII with "collarlike" subdivision (Fig. 73). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Limonicola* . . . 7
2. *General.*—Mandibles well developed, laciniae long and whiplike; palpus composed of two elongate segments (Fig. 59). *Terminalia.*—Apex of thumblike inner sublobe of hypogynial lobe spiculate. . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
   *General.*—Mandibles absent, laciniae very short and stubby; palpus a single diminutive segment (Fig. 2). *Terminalia.*—Apex of thumblike inner sublobe of hypogynial lobe denticulate. . . 4
3. *General.*—Lateral margin of mandible with numerous fine spiculae (Fig. 59). *Terminalia.*—Spermathecae elongate, ducts very short. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. inca*
   *General.*—Lateral margin of mandible with a few denticulae only (Fig. 80). *Terminalia.*—Spermathecae spherical, ducts very long, curving around and adnate to corpus. . . . . *P. andeana*
4. *General.*—Claws on all legs short, curved, with sub-basal tooth (Fig. 31). *Terminalia.*—Medial depression of sternite VIII acutely V-shaped (Fig. 14). Lateral margin of VIIIth sternite lobe curved strongly, apex closely appressed to base of hypogynial plate; lobe usually with only 5–6 setae (up to 10 rarely), restricted to its central surface (Fig. 14). . . . . . . . *P. aspergonympha*
   *General.*—Claws on all legs long, slender, sigmoidally curved (Fig. 4). *Terminalia.*—Medial depression of sternite VIII U-shaped (Fig. 13) to broadly V-shaped (Fig. 15). Lateral margin of VIIIth sternite lobe straight to curved, if latter then apex not closely appressed to base of hypogynial plate; lobe with 11–30 setae, usually 12–20 and often extending onto membrane at base of lobe (Fig. 15). . . . . . . . . . . 5
5. *General.*—Ultimate antennal segment longer (1.3) than penultimate. *Terminalia.*—Ventrolateral surface of inner thumblike lobe of hypogynial lobe with acutiform scalelike teeth. Internal sclerotization at base of medial depression of sternite VIII a narrow, elongate bar. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. roldani*
   *General.*—Length of ultimate antennal segment equal to penultimate. *Terminalia.*—Ventrolateral surface of inner thumblike lobe of hypogynial lobe with microtrichia. Internal sclerotization at base of medial depression of sternite VIII lanceolate or broad. . . . . . . . . 6
6. *General.*—No characters. *Terminalia.*—Internal sclerotization at base of medial depression of sternite VIII wide, lanceolate (Fig. 15). . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. charadrae*
   *General.*—No characters. *Terminalia.*—Internal sclerotization at base of medial depression of sternite VIII wide, subquadrate (Fig. 16). . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. eldorado*
7. *General.*—Ultimate segment of antenna elongate, irregularly shaped (Fig. 103). *Terminalia.*—No characters. . . . . . . . . . . *L. astylis*
   *General.*—Ultimate segment of antenna subequal to penultimate (usually slightly smaller) (Fig. 107). *Terminalia.*—No characters. . . 8
8. *General.*—5th tarsomere of hind leg with weak pollex (Fig. 109). *Terminalia.*—Apex of VIIIth sternite lobe produced, broad (Fig. 110). Dorsal division of lobe of hypogynial plate long and slender (Fig. 110). . . . . . . . . . . . . . *L. medius*
   *General.*—5th tarsomere of hind leg without pollex (Fig. 87). *Terminalia.*—Apex of VIIIth sternite lobe not produced, acute (Fig. 72). Dorsal division of lobe of hypopygial plate short and broad (Fig. 72). . . . . . . . . . . . . . . . . . 9

9. *General.*—No characters. *Terminalia.*—Apex of lobe of sternite VIII slightly incurved. .... .................................*L. davila*
   *General.*—No characters. *Terminalia.*—Apex of lobe of sternite VIII straight. .. *L. lichanos*

**Immatures**

Because the larval and pupal stages of the two genera do not segregate by any reliable characters in parallel with the adult male dichotomy, the following keys run directly to species.

*Pupae (*Paltostoma saltana, Limonicola astylis, *and* L. kolomeros *unknown)*

It is important in some cases to distinguish carefully between males and females when attempting to identify pupae with the key, because characteristics of one or the other sex of one species may resemble the opposite sex of another species. When the terminalia of pharate adults are not available within the pupal case, or eggs present, the sexes may be distinguished as follows: female pupae are generally larger (some exceptions) than male pupae and less angular. The apices of the fore and mid leg cases extend less than that of the hind leg (not reaching the posterior rim) in females; the leg cases are all long and approximately coterminate in males.

1. Integument hirsute, densely covered with bristlelike spines (Fig. 51). ..........*P. andeana*
   Integument papillose (Fig. 18). ........... 2
2. Posteriormost branchial lamellae strongly convergent, often contiguous. Outer plates triangular (Fig. 48). ...... (most *Paltostoma*) ... 3
   Posteriormost branchial lamellae parallel to divergent. Outer plates elongate (Fig. 97). ..... ................... (most *Limonicola*) ... 5
3. Papillae minutely spinulate (Fig. 21, inset). ... ...................... *P. aspergonympha*
   Papillae smoothly rounded .............. 4

Note: The following two species are very similar and difficult to distinguish. Only relative characteristics are available. The males are more distinctive than the females, having the following features the more acutely developed:

4. Anterior branchial plates parallel, apices slightly twisted to bring outer margins dorsad, acuminate; posterior plates usually contiguous apically (Fig. 45). Smaller (length usually less than 4 mm). .......................... *P. charadrae*
   Anterior branchial plates divergent, apices not twisted, acute; posterior plates convergent only (Fig. 47). Larger (length usually greater than 4 mm). ....................... *P. eldorado*
5. Lateral margins of abdominal segments IV–VI with small cusps (Fig. 18). Posterior prolongation of posterior branchial plate swollen and joining similar convexity of branchial sclerite to form compound bulla (Fig. 17). ... *P. roldani*
   Lateral margins of abdominal segments entire, without cusps. Posterior prolongation of posterior branchial plate bullate but not joined to similar convexity of branchial sclerite. ..... 6
6. Abdominal tergites raised middorsally. .... 7
   Abdominal tergites planate middorsally. ..... ................................*L. davila*
7. Scutum sparsely papillose, papillae restricted to posterior region only. Medial dorsal ridge of abdomen continuous, itself with a medial depression (Fig. 49). Outer branchial plates with broad membranous border on inner side (Fig. 50). ........................... *P. inca*
   Scutum densely papillose over entire area. Raised middorsal portion of abdomen broken into a discontinuous series of low bosses. Outer branchial plates entirely sclerotized. .......... 8

Note: The following two species have very similar pupae. The differences noted here are tentative because of inadequate material of *L. medius.*

8. Outer margin of anterior lamellar plate excavated at base; bulla at base of lamellae large and hemispherical (Fig. 100). ......... *L. medius*
   Outer margin of anterior lamellar plate entire; bulla at base of lamellae moderately large, and slightly flattened (Fig. 99). ....... *L. lichanos*

*Fourth-instar larvae (*Limonicola astylis, L. medius, *and* L. kolomeros *unknown)*

1. Dorsal pseudopod VII very small and inserted almost completely into posterior margin. Anterior and posterior margins of abdominal segments often angular, in contact when larva contracted ("onisciform shape"). Area medial to base of pseudopod ventrally with scattered small setae. Anterior and posterior lines of heavy modified setae on conoid convexities, curving laterally into base of dorsal pseudopod (=circumlateral series) (Fig. 56). ............... ................ (mostly *Paltostoma*) ... 2
   Dorsal pseudopod VII well developed and projecting free of posterior margin. Anterior and posterior margins of abdominal segments smoothly rounded, a wide space between segments when larva contracted ("lobular shape"). Area medial to base of pseudopod ventrally with patch of dense denticles. Modified dorsal setae mostly small and setiform (circumlateral series absent) (Fig. 101). .................. ............... (mostly *Limonicola*) ... 7
2. Dorsa of abdominal segments I–VI each with pair of large, dorsolateral, sclerotized, smooth, erect, spinelike projections, with sharply acute apices (Fig. 74). ................. *P. inca*
   Dorsa of abdominal segments I–VI not produced. ............................ 3
3. Basal antennal segment elongate, 0.7–1.0 length of distal (Fig. 88). ............. *P. andeana*
   Basal antennal segment very short, never more than 0.2 length of distal (Fig. 56). ....... 4

4. Several dorsal modified sensilla conspicuously larger than others and coniform (Figs. 25, 32). ...................... *P. aspergonympha*
Dorsal modified sensilla all more or less equal in size and shape. ...................... 5
5. Terminal lobe tapering and narrow posteriad, border not deeply pigmented. Circumlateral series ill-defined, mostly lateral (Figs. 26, 53). ........................... *P. charadrae*
Terminal lobe broad throughout, border deeply pigmented (black). Circumlateral series of modified setae well developed, extensive mediad. (Figs. 56, 57). .................... 6
6. Lateral margin of abdominal segment VII slightly concave anterior to dorsal pseudopod (Fig. 56). Pseudopod I elongate. ........... ........................... *P. eldorado*
Lateral margin of abdominal segment VII strongly excised anterior to dorsal pseudopod (Fig. 57). Pseudopod I barely longer than broad. .............................. *P. saltana*
7. Terminal lobe tapering and narrow posteriad, border not pigmented. ................. 8
Terminal lobe broad throughout, border deeply pigmented (black). .................. 9
8. Dorsolateral portions of abdominal segments II–VI drawn out into prominent, upward arching prolongations (Fig. 23). Dorsa of prothoracic region and lateral portions of abdominal segments with linear series of clavate (modified) setae (Fig. 24). ................. *P. roldani*
Dorsa of abdominal segments II–VI planate, without protuberances of any kind (Fig. 122). Dorsa of prothoracic region and lateral portions of abdominal segments densely set with ascinaciform (modified) setae (Fig. 124). .... .................... *L.* unidentified larva 1
9. Dorsa of abdominal segments I–VI each with a central boss. Terminal lobe very broad, strongly arcuate, terminal incision very narrowly V-shaped (Fig. 101). ......... *L. lichanos*
Dorsa of abdominal segments I–VI planate, without a central boss. Terminal lobe moderately broad, slightly curved, terminal incision broadly U-shaped. ................... 10
10. A conspicuous seta on lateral margin of terminal lobe (Fig. 123). . *L.* unidentified larva 2
Lateral margin of terminal lobe non-setose (not figured). ....................... *L. davila*

## SYSTEMATICS

The Blephariceridae of Antioquia Department are placed in *Paltostoma* and *Limonicola*, the former provisionally. These apistomyiine genera along with the Brazilian *Kelloggina* Williston, 1907, are currently under study by Hogue, who has found them in need of revision and reclassification. *Paltostoma*, in particular, consists of a varied assemblage and may possibly require division. Many of the species exhibit medial structures in the male terminalia considerably different from those of the type species. The distinction even from *Limonicola*, the best defined genus, is obscured by sharing of larval types with *Paltostoma*. For example, this stage of *Limonicola lichanos* is of the type normal to *Paltostoma*, whereas the pupa and adults clearly resemble those of *Limonicola*.

The two genera and all neotropical blepharicerids are referred to the tribe Apistomyiini for the present. The tribe is considered in its broad sense to include the Paltostomatini, whose monophyly and distinctiveness has not yet been adequately demonstrated.

## APISTOMYIINI

## PALTOSTOMA Schiner

*Paltostoma* Schiner, 1866:931. Type species: *Paltostoma superbiens* Schiner, 1866.

*Paltostoma* is currently an ill-defined genus used for most neotropical apistomyiine species that do not fall readily into the other genera. Most larvae have a very small dorsal pseudopod VII and conspicuous circumlateral series of secondary sensilla, pupa with more or less triangular outer branchial plates, the posterior pair convergent, adult mouthparts usually well developed, male terminalia with thin-walled aedeagal rods lacking inner canals, lateral tines usually present, and female terminalia with medial depression of sternite VIII with a "collar-like" subdivision. (See Keys for more characteristics.)

The name refers to the much elongated, slender proboscis of the males of most species (Greek *palton* = spear + *stoma* = mouth); its gender is neuter.

### 1. *Paltostoma roldani*
### Hogue and Bedoya,
### new species

Figures 1–8, 13, 17–19, 23, 24

*Limonicola* sp. 3 of Bedoya, 1984. Bedoya and Roldán, 1984:118, fig. 4a. Roldán, 1988: fig. 143. [Determinations based on larvae.]

**DIAGNOSIS.** *Adult.*—By external features, adults of *P. roldani* are indistinguishable from those of *P. eldorado* (both with a single palpal segment and ultimate antennal segment longer than penultimate). Features of the terminalia are distinctive, however, the outer aedeagal rods arise laterally from the sperm sac and curve gently rather than arising directly from the posterolateral corners; also, the shape of the male's outer gonostylus is distinctive (apex bent down at a right angle). In the female the thumblike lobe of the hypogynial plate bears acutiform scalelike teeth not found in *P. eldorado*. *Pupa.*—This stage is unique among Blephariceridae in the possession of cusps on the outer margins of the abdominal tergites. *Larva.*—The larva is immediately recognizable by the large, blunt, porrect projections from the dorsolateral portions of abdominal segments II–VI.

**DESCRIPTION. Male** (Figs. 1, 3, 5–8). Robust, well sclerotized, with especially stout hind legs.

*Coloration.* Ground color rich, velvety chocolate-brown, darker and tending toward black on anterior portion of scutum. Head capsule and thorax with silvery pollinosity, forming irregularly appearing and disappearing patches as specimen is rotated in light from certain angles; supraalar sclerites dull in contrast to other sclerites. Legs and abdomen, including terminalia, dull, without evident pollinosity; abdominal tergites tending to light orange-brown anteriorly. Wing membrane infuscate. *Size.* A medium-sized blephariceride. Measurements (N = 3–4): wing length 6.0 (6.0–6.0). Leg segment lengths:

| | | fore leg |
|---|---|---|
| femur | | 2.7 (2.6–2.8) |
| tibia | | 2.9 (2.8–3.0) |
| tarsus | 1 | 1.9 (1.9–2.0) |
| | 2 | 0.82 (0.80–0.84) |
| | 3 | 0.47 (0.42–0.50) |
| | 4 | 0.24 (0.20–0.26) |
| | 5 | 0.30 (0.28–0.32) |

| | | mid leg |
|---|---|---|
| femur | | 3.5 (3.5–3.6) |
| tibia | | 3.0 (2.8–3.1) |
| tarsus | 1 | 1.9 (1.8–1.9) |
| | 2 | 0.78 (0.74–0.82) |
| | 3 | 0.46 (0.44–0.48) |
| | 4 | 0.24 (0.20–0.26) |
| | 5 | 0.31 (0.30–0.32) |

| | | hind leg |
|---|---|---|
| femur | | 4.9 (4.8–5.0) |
| tibia | | 4.5 (4.4–4.7) |
| tarsus | 1 | 2.2 (2.2–2.3) |
| | 2 | 0.69 (0.66–0.70) |
| | 3 | 0.42 (0.40–0.45) |
| | 4 | 0.25 (0.24–0.26) |
| | 5 | 0.27 (0.26–0.28) |

*Head* (Fig. 1). Normal type, subholoptic. Eyes approximate dorsally, interocular distance equal to combined diameters of five ommatidia; anterior margin of eye smoothly curved. Mouthparts well developed, proboscis very long, labium about 1.6 head width; palpus very short, a single elongate segment clearly evident (=segment 3), sensory pit present; a basal segment partly developed, 0.5 length of segment 3. Antenna 15-segmented, flagellar segments elongate barrel-shaped; ultimate segment elongate, longer (1.6–1.8) than penultimate, proportions of apical three segments 1.0–1.0–1.6 to 1.8.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few and scattered; occipitals numerous (13–16); labrals numerous, scattered, on basal half only; labials and labellars numerous, scattered throughout.

*Thorax and appendages* (Fig. 3). Anal angle of wing produced, lobular. Legs somewhat heavier than in most Apistomyiini, hind legs considerably stouter than other legs. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg 1.1–0.7–0.4–0.6–0.5–1.3, mid leg 0.9–0.6–0.4–0.6–0.5–1.3, hind leg 0.9–0.5–0.3–0.6–0.6–1.1; tarsomere 4 short in relation to 3 in all legs (0.5–0.6). Tarsomeres 5 similar on all legs, curved, with pollex of heavy setae; claw sickle-shaped, trichiate basally, with sub-basal tooth.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; short dorsocentral series; supraalars and prescutellars absent; scutellars numerous, long and concentrated in an elongate, dense brushlike group laterally, none medially; preepisternals several (5–8); metapleurals numerous (18); suprametapleurals few (4–5).

*Terminalia* (Figs. 5–8). Cerci parallel; interlobular depression shallow, V-shaped; individual cercus broadly triangular. Lateral walls of subanal pouch heavily sclerotized and connected to posterior arm of gonite by a stout arm. Apex of tegmen with dorsal recurved keel. Outer gonostylus large, a simple rectangular lobe, apex bent ventrad at right angle. Inner gonostylus elongate, erect, digitiform (apex slightly dilated). Expanded bases of aedeagal rods lacking internal spinules. Outer rods leaving sperm sac at the side and basally arcuate. Lateral tine attenuate, with numerous small spines at base.

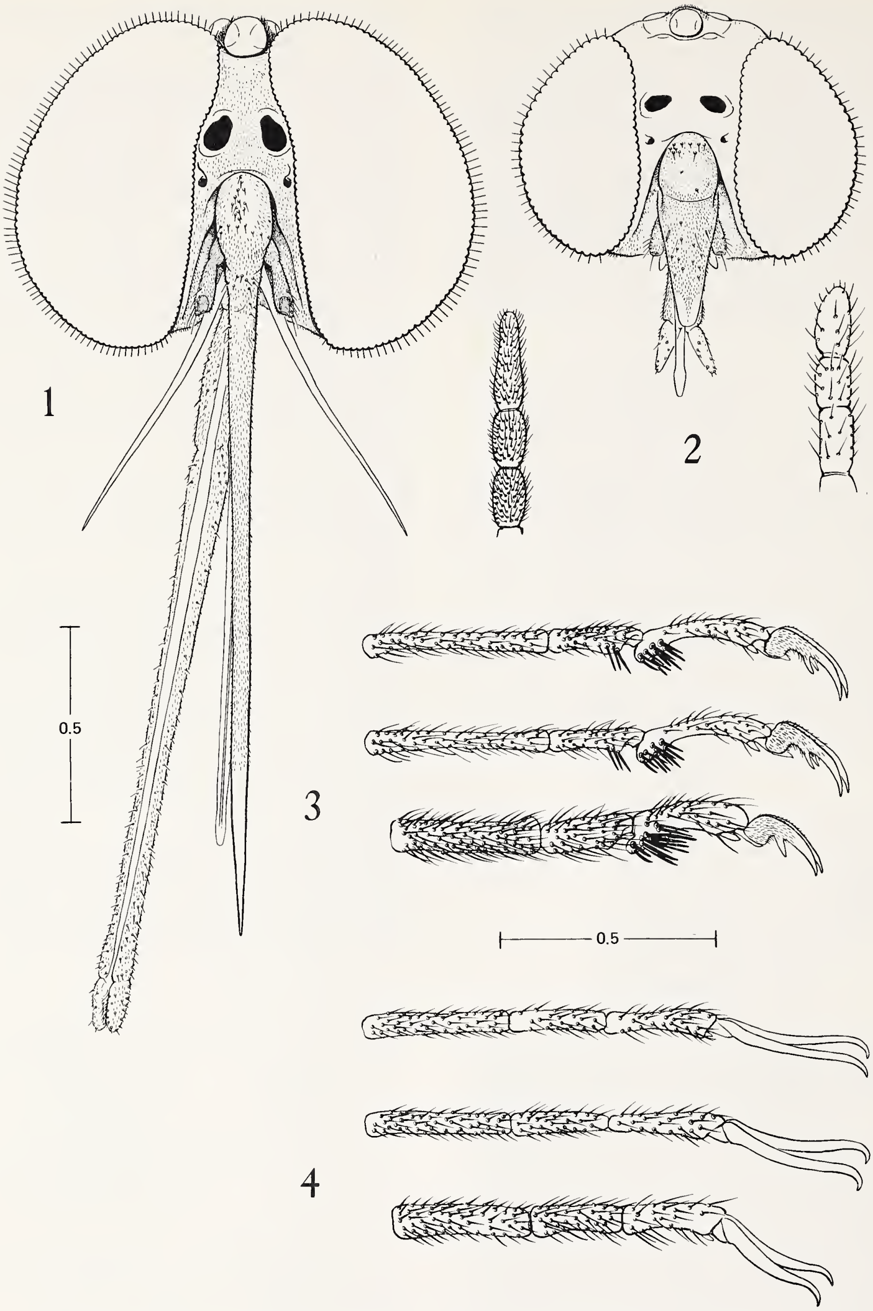
Sensilla.—Epandrium with transverse series of numerous medium to large setiforms. Cercus generally with mixed small to medium setiforms; setae of inner arm nearly complete to apex. Outer gonostylus with medium setiforms general ectally; sparse basal and apical groups entally. Alveoliform sensilla of Xth tergite not apparent. Xth sternite with two long setiforms apically.

**Female** (Figs. 2, 4, 13). *Coloration.* As in male. Wing membrane infuscate. *Size.* A medium-sized blephariceride. Measurements (N = 2): wing length 6.5 (6.2–6.8). Leg segment lengths:

| | | fore leg |
|---|---|---|
| femur | | 2.1 (2.0–2.2) |
| tibia | | 2.0 (1.9–2.0) |
| tarsus | 1 | 1.3 (1.2–1.4) |
| | 2 | 0.55 (0.50–0.61) |
| | 3 | 0.34 (0.32–0.37) |
| | 4 | 0.23 (0.22–0.24) |
| | 5 | 0.26 (0.24–0.28) |

| | | mid leg |
|---|---|---|
| femur | | 3.1 (2.9–3.3) |
| tibia | | 2.1 (2.1–2.2) |
| tarsus | 1 | 1.4 (1.3–1.5) |
| | 2 | 0.55 (0.48–0.61) |
| | 3 | 0.34 (0.32–0.37) |
| | 4 | 0.23 (0.22–0.24) |
| | 5 | 0.27 (0.27–0.28) |

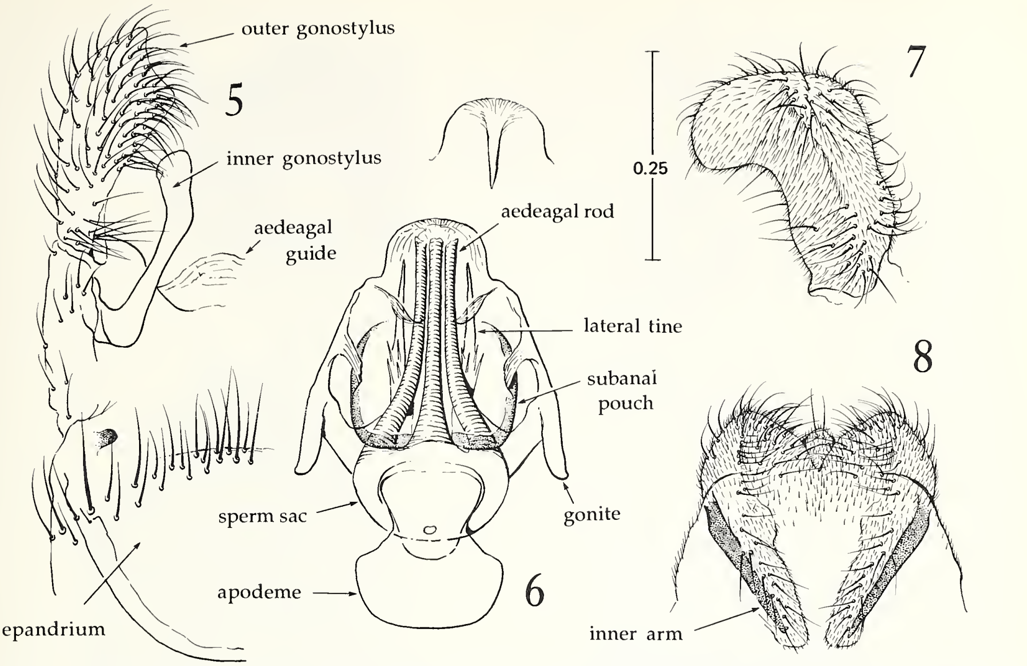
| | | hind leg |
|---|---|---|
| femur | | 4.3 (4.2–4.4) |
| tibia | | 3.9 (3.9–3.9) |
| tarsus | 1 | 2.0 (1.9–2.2) |
| | 2 | 0.70 (0.64–0.75) |
| | 3 | 0.39 (0.38–0.40) |
| | 4 | 0.24 (0.22–0.25) |
| | 5 | 0.26 (0.26–0.26) |



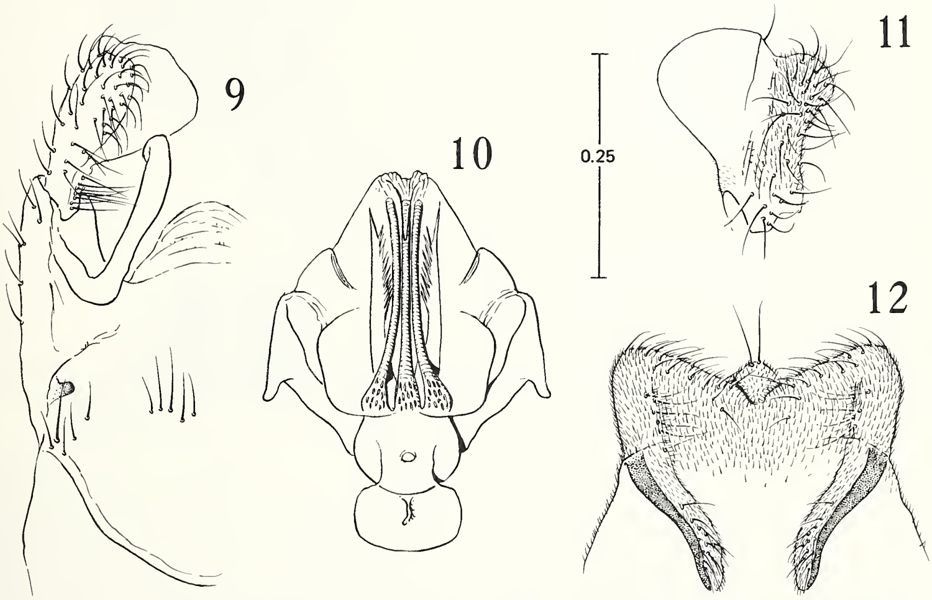
**Figures 1–4.** *Paltostoma roldani.* **1.** Male head (frontal view) and terminal antennal segments (inset). **2.** Female head and terminal antennal segments (arrangement as for male). **3.** Terminal tarsal segments of male (fore leg, upper; mid leg, center; hind leg, lower; lateral view). **4.** Terminal tarsal segments of female (arrangement as for male).

*Head* (Fig. 2). Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance equal to 0.3 width of head capsule. Mouthparts well developed; mandibles absent, lacinia very short; proboscis very short, labium about 0.3 width of head capsule; margin of hypopharynx entire, apex of labrum rounded to truncate; palpus very short, a single diminutive segment; sensory pit present. Antenna 15-segmented, flagellar segments elongate cylindrical, ultimate segment slightly longer (1.3) than penultimate, proportions of apical three segments 1.0–1.0–1.3.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few, scattered, small; occipitals several (5–8), extending dorsad to near vertex; postgenals few (2–5); labrals several to numerous, scattered midlength; labials and labellars several, scattered.



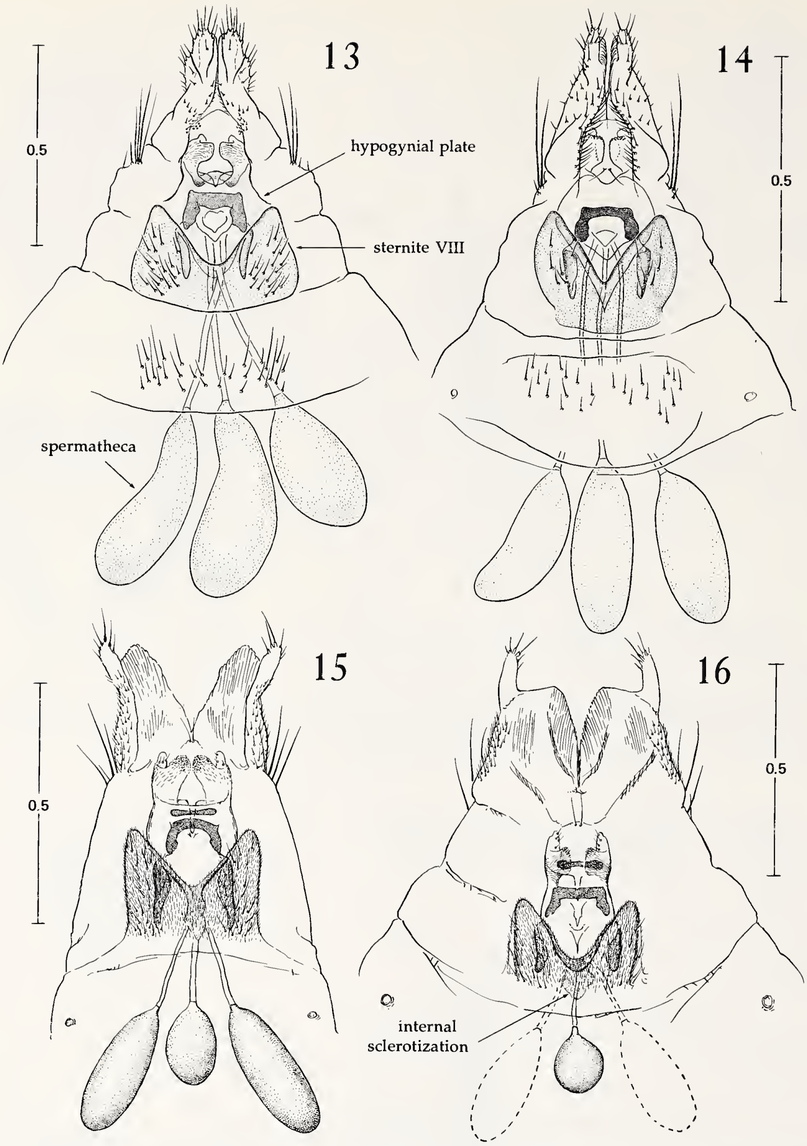
**Figures 5–8.** *Paltostoma roldani,* male terminalia (dorsal views), anatomical details labeled. **5.** Genital capsule and gonostyli. **6.** Mesosomal structures and gonites. **7.** Left outer gonostylus (inner view). **8.** Cercal complex.



Figures 9–12. *Paltostoma aspergonympha,* male terminalia (dorsal view). **9.** Genital capsule and gonostyli. **10.** Mesosomal structures and gonites. **11.** Left outer gonostylus (inner view). **12.** Cercal complex.

*Thorax and appendages* (Fig. 4). Anal angle of wing produced, lobular. Legs long and slender, hind legs especially stout. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg 0.9–0.7–0.4–0.6–0.7–1.1, mid leg 0.9–0.6–0.4–0.6–0.5–1.3, hind leg 0.9–0.5–0.3–0.6–0.6–1.1; tarsomere 4 short in relation to 3 on all legs (0.5–0.7). Tarsomeres 5 similar on all legs, curved, with weak pollex of heavy setae; claws simple, long, slender and gently sigmoidally curved, non-trichiate.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; dorsocentral series complete; supraalars and prescutellars absent; scutellars very numerous, long and concentrated in an



**Figures 13–16.** *Paltostoma,* female terminalia (ventral view). **13.** *P. roldani,* anatomical details labeled. **14.** *P. aspergonympha.* **15.** *P. charadrae.* **16.** *P. eldorado.*

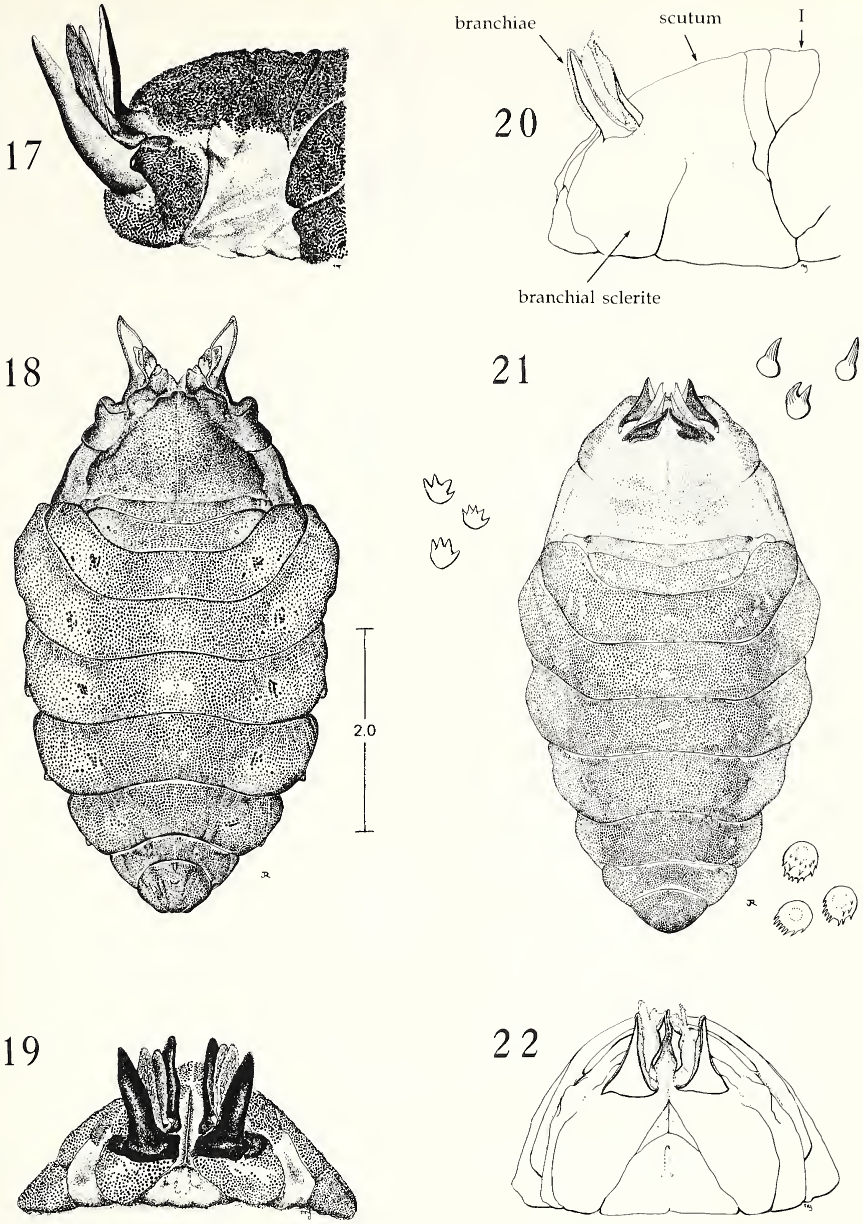
elongate, brushlike group laterally, none medially; preepisternals few (4); metapleurals several to numerous (11–14); suprametapleurals several (6).

*Terminalia* (Fig. 13). VIIIth sternite well sclerotized throughout, base broad, lateral margin curved; medial depression deep, U-shaped, internal sclerotization flat, narrow, fusiform; lobe straight, apex not appressed to hypogynial plate. Hypogynial plate complex, base much broader than lobes; lobe with narrowed neck, dorsal division short, lobulate, nude, ventral division with strong longitudinal striae becoming acute spinuliforms distad. Spermathecae three, all large, weakly sclerotized, two similar, elongate oviform, third about two-thirds size of others, oviform; necks very short and straight.

Sensilla.—Sternite VIII with 15–20 medium setiforms general over lobes and base laterally.

**Pupa** (Figs. 17–19). *Integument.* Periphery rounded, sclerotized integument underfolded and forming broad ventral border. Papillose dorsally. Papillae even and very dense (individual papillae nearly touching each other). Individual papillae small, smooth, rounded, oval convexities; larger on scutum and branchial sclerite. Papillar distribution as follows: scutum—dense over entire disc; branchial sclerite—dense over entire posterodorsal convexity (except anteriorly) and on ventral fold only; metathoracic and abdominal tergites—even and dense over entire dorsum.

*Size.* Medium for family. Measurements, male



**Figures 17–22.** *Paltostoma*, pupae. **17.** *P. roldani*, anterior portion, lateral view. **18.** Same, entire, dorsal view. **19.** Same, frontal view. **20.** *P. aspergonympha*, anterior portion, lateral view, anatomical details labeled. **21.** Same, entire, dorsal view; detail of cuticular papillae (insets). **22.** Same, frontal view.

(N = 10): length 5.3 (4.6–5.8), width 3.3 (2.8–3.6); female (N = 10): length 5.9 (5.2–6.5), width 3.8 (3.4–4.3). Male about 0.8 size of female.

*General.* Outline shape oval, margins irregular; abruptly widened laterally at abdominal segment III in both sexes. L/W male = 1.6, female 1.6. Shape in cross section moderately convex, sides declivous all around. Dorsal sclerites: branchial sclerite longer than tall, complex, with a dorsal convexity that joins basiposterior bulla of first branchial lamella; acutely folded along ventral margin. Anterior margin of scutum sharply precipitous, with weakly trilobed anterior margin. Suture separating metathoracic sclerite from abdominal tergite I angulate medially. Lateral margins of abdominal tergites projecting equally, margins of III–VI each usually with a small but conspicuous cusp or tooth just posterior to midpoint (cusp rarely absent).

*Branchiae.* Large, porrect, slightly divergent. Outer plates elongo-triangular, with semi-acute apices; inner two plates similar to outer but slightly smaller; anterior plate largest; anterior and posterior plates with strongly expanded bases; posterior expansion of the anterior plate bullate, joining dor-

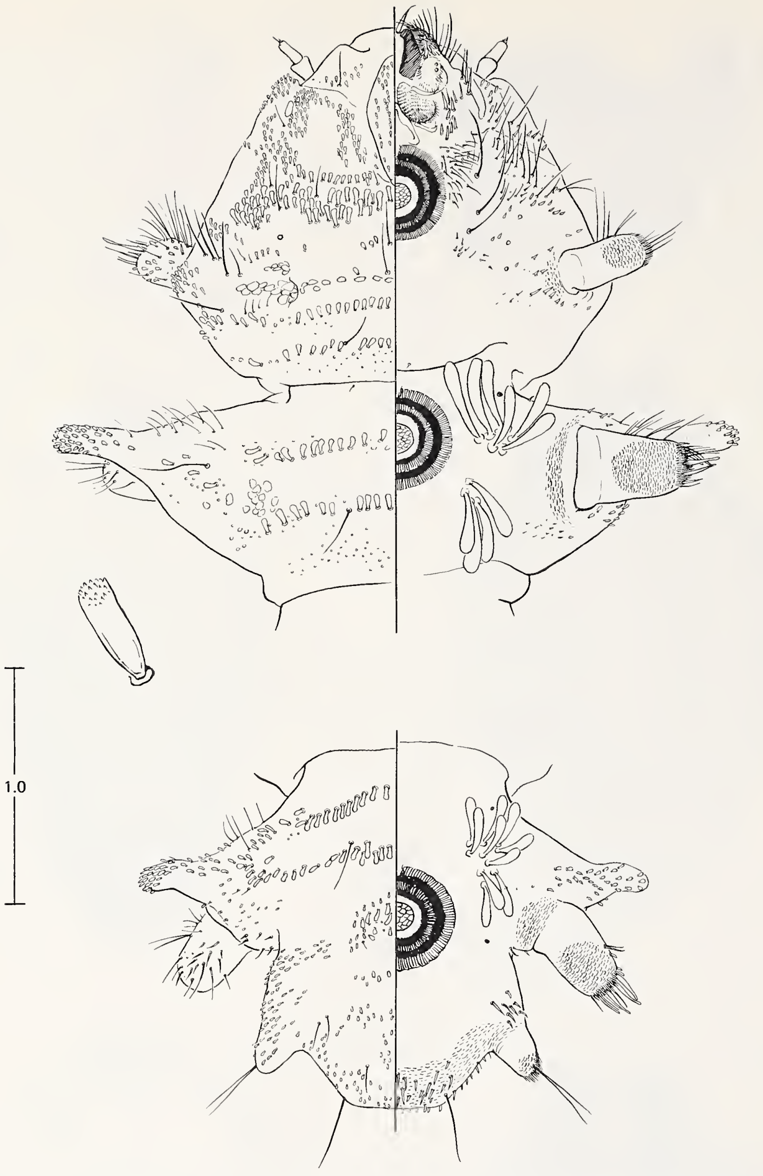


**Figure 23.** *Paltostoma roldani,* larva (dorsal view, left; ventral view, right; typical modified sensillum, inset).

sal convexity of branchial sclerite; bases of anterior lamellae approximate, apices divergent.

**Larva** (Figs. 23–24). *General.* Body form complex lobiform. Outline shape of anterior division angular, subhexagonal.

*Integument.* Dorsum moderately well sclerotized. Corrugations distinct, fine, linear and arranged in circular pattern around transverse rows of modified sensilla, becoming zig-zagging between these sensilla; corrugations ringing dorsolateral prominences. Venter with imbricate patches curving concentrically around bases of pseudopods.

*Coloration.* Trunk pigmentation even, light brown; sclerotized portions pale brown.

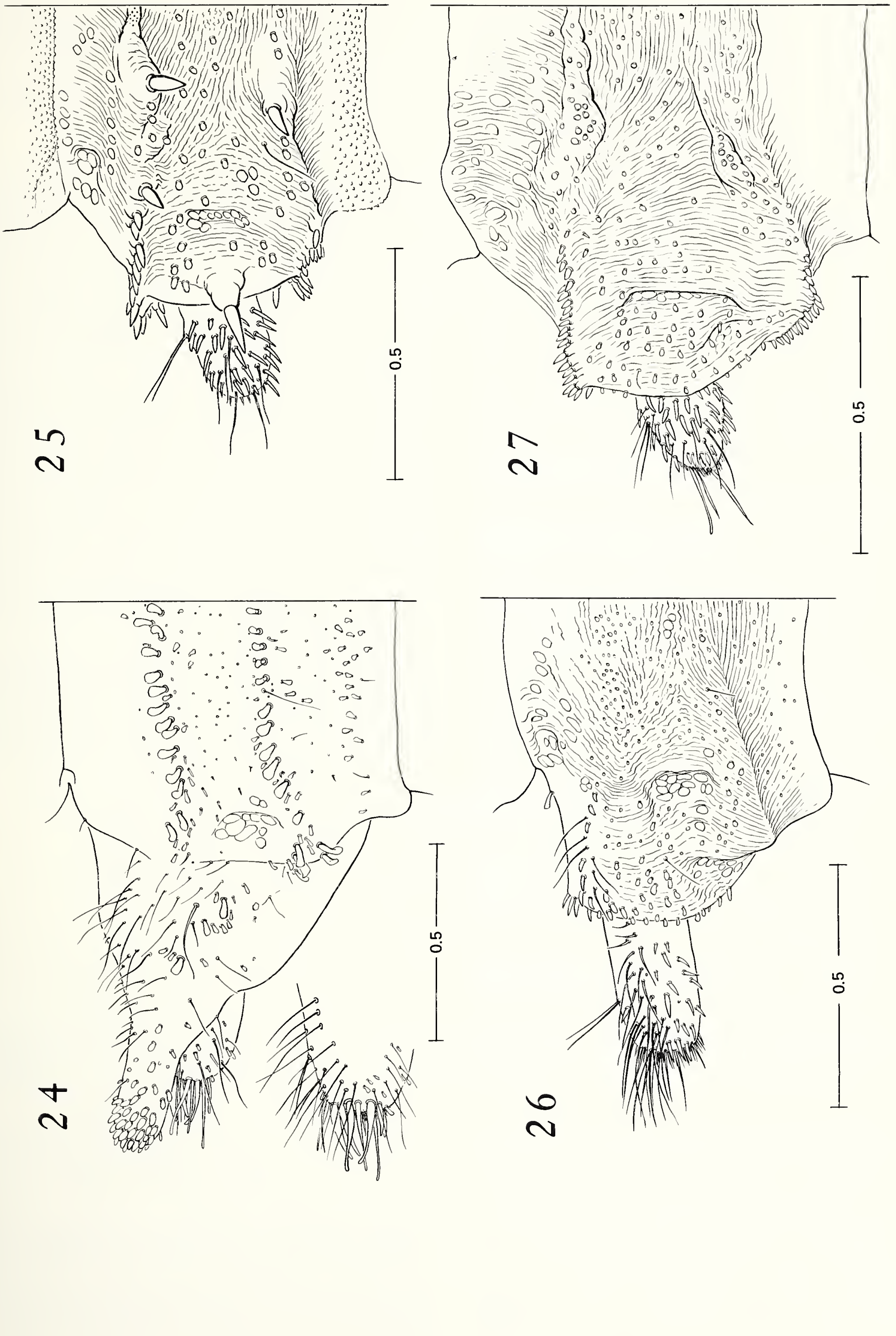
*Size.* Medium for the family. Measurements (N = 10): body length 7.8 (7.3–8.7), head capsule width 1.7 (1.6–1.9), antennal segment lengths, basal 0.08 (0.07–0.09), apical 0.14 (0.13–0.15).

*Head.* Antennal segment proportions 1.0–1.9.

*Trunk.* Mediolateral portions of abdominal dorsum drawn outward and upward into long, upcurving, conical projections (similar to dorsal pseudopods but arising in dorsolateral area of segment, far removed from morphological position of those structures). No other dorsal sclerotizations present.

*Anal division.* Dorsal pseudopod a large, conical lobe directed posterolaterad. Terminal incision V-shaped, open and spacious. Terminal lobe narrowed apically, posterior margin straight.

*Primary sensilla* (medium setiforms unless otherwise described). tM–T in line, well spaced. stM–T lateral to t, small, pyriform. Inner tpP anterior



**Figures 24–27.** *Paltostoma* larvae, abdominal segment III (left half, dorsal view). **24.** *P. roldani.* **25.** *P. aspergonympha.* **26.** *P. charadrae.* **27.** *P. eldorado.*

to spiracle. Outer tpI–VI indiscernible. Terminal setae 1–1, long, widely separated.

*Dorsal modified sensilla.* Small, obovate types in rows on head sclerites. Numerous large modified sensilla of special form (elongate, with spatulate, denticulate apex) distributed in transverse, anterior and posterior, monolinear rows on segments I–VI, these losing regularity laterally, becoming scattered and mixed with small setiforms. These large sensilla also present on prothorax, but not arranged linearly. Dense clusters of small, elongate glandiforms and elongate oviforms on apices of dorsolateral projections. Dorsal sensilla of pseudopods setiform posteriorly, small oviforms anteriorly; several curved, blunt-tipped chaetiforms/taeniaforms apically. Integument set with general background field of very small, fine setiforms.

**SPECIMENS EXAMINED.** Types: HOLOTYPE male (terminalia mounted on slide no. CLH 86-603); ALLOTYPE female (terminalia mounted on slide no. CLH 87-178); 3 male and 3 female PARATYPES: COLOMBIA, *Quindio,* Quebrada Salado, 4 km E Calarcá, 20 Jun 1984, C.L. Hogue, CLH 338 (LACM) (1 female with terminalia mounted on slide no. CLH 85-185, 2 females, still in pupal cases, with heads mounted on slides nos. 87-13 and 87-14).

**Additional Specimens.** COLOMBIA, *Antioquia,* no specific locality, Aug 1983 I. Bedoya 4 (2 larvae). Quebrada Iguaná, 13 Jun 1984, C.L. Hogue, CLH 323 (18 larvae, 3 pupae). Quebrada La Cascada, 13 Jun 1984, C.L. Hogue, CLH 324 (2 pupae). Quebrada La Cascada, 13 Jun 1984, C.L. Hogue, CLH 324.1 (46 larvae). Quebrada Piedra Blanca, 12 km W Guarne, 8 Jan 1986, C.L. Hogue, CLH 347.1.2 (7 larvae, 55 pupae). Quebrada La Espadera, 7.7 km E Medellín, 23 Jun 1983, C.L. Hogue, CLH 308 (10 pupae). Quebrada La Cascada, 9.1 km E Medellín, 23 Jun 1983, C.L. Hogue, CLH 309.1, 309.2 (2 larvae, 22 pupae). Quebrada La Cascada, 9.1 km E Medellín, 23 Jun 1983, C.L. Hogue, CLH 309.3 (2 larvae). Quebrada El Treinta, 2 km N Palmitas, 22 Jun 1983, C.L. Hogue, CLH 303 (19 pupae). Quebrada El Treinta, 2 km N Palmitas, 12 Jun 1984, C.L. Hogue, CLH 320 (7 larvae); 1 km SE Paso de Boquerón, 22 Jun 1983, C.L. Hogue, CLH 300 (7 larvae, 12 pupae). Quebrada La Hundida, 16.8 km E Santuario, 8 Jan 1986, C.L. Hogue, CLH 348.2 (1 larva). Quebrada Cadavid, 17.9 km E Santuario, 8 Jan 1986, C.L. Hogue, CLH 349.1.2 (13 larvae).

*Quindio,* same data as types (188 larvae, 46 pupae).

*Valle,* Quebrada Honda, Peñas Blancas, 1800 m, 3 Jun 1974, C.L. Hogue (1 larva, 1 pupa).

**ETYMOLOGY.** The species is named for Dr. Gabriel Roldán, in recognition of the multitude of his unmatched contributions to the study of the aquatic insects of Antioquia Department.

**REMARKS.** Association of the stages of *P. roldani* is certain: larva–pupa–adults by the ontogenetic method.

As seen from the collection records this is a fairly widespread and common species. It is also conspicuous because of its relatively large size. Our collections contain another species with similar larvae except for the slightly less developed dorsolateral projections and chaetotactic differences; it is unnamed and not found in Antioquia Department.

The holotype and two paratypes were found by Hogue trapped in a spider web over a small stream.

## 2. *Paltostoma aspergonympha* Hogue, new species

Figures 9–12, 14, 20–22, 28–32

**DIAGNOSIS.** *Adult.*—The female of this species is unique among regional *Paltostoma* in the dissimilarity of the fore tarsi to the mid and hind tarsi: fore tarsomere 5 is unusually long, straight, without a pollex, and bears simple claws; tarsomeres 5 on the other legs are relatively short, curved, with a basal pollex of heavy setae, and bear claws with a sub-basal tooth. This is the only regional *Paltostoma* with spinules on the inner walls of the sperm sac and bases of the aedeagal rods; the lobes of the VIIIth sternite of the female terminalia are distinctive, with a curved lateral margin, the apex closely appressed to the the base of the hypogynial plate. *Pupa.*—Only the pupa of this *Paltostoma* have denticulate, rather than smoothly rounded, papillae. *Larva.*—The larva is distinguished from other regional *Paltostoma* by the presence of conspicuously large and heavy, coniform, secondary sensilla on the dorsum.

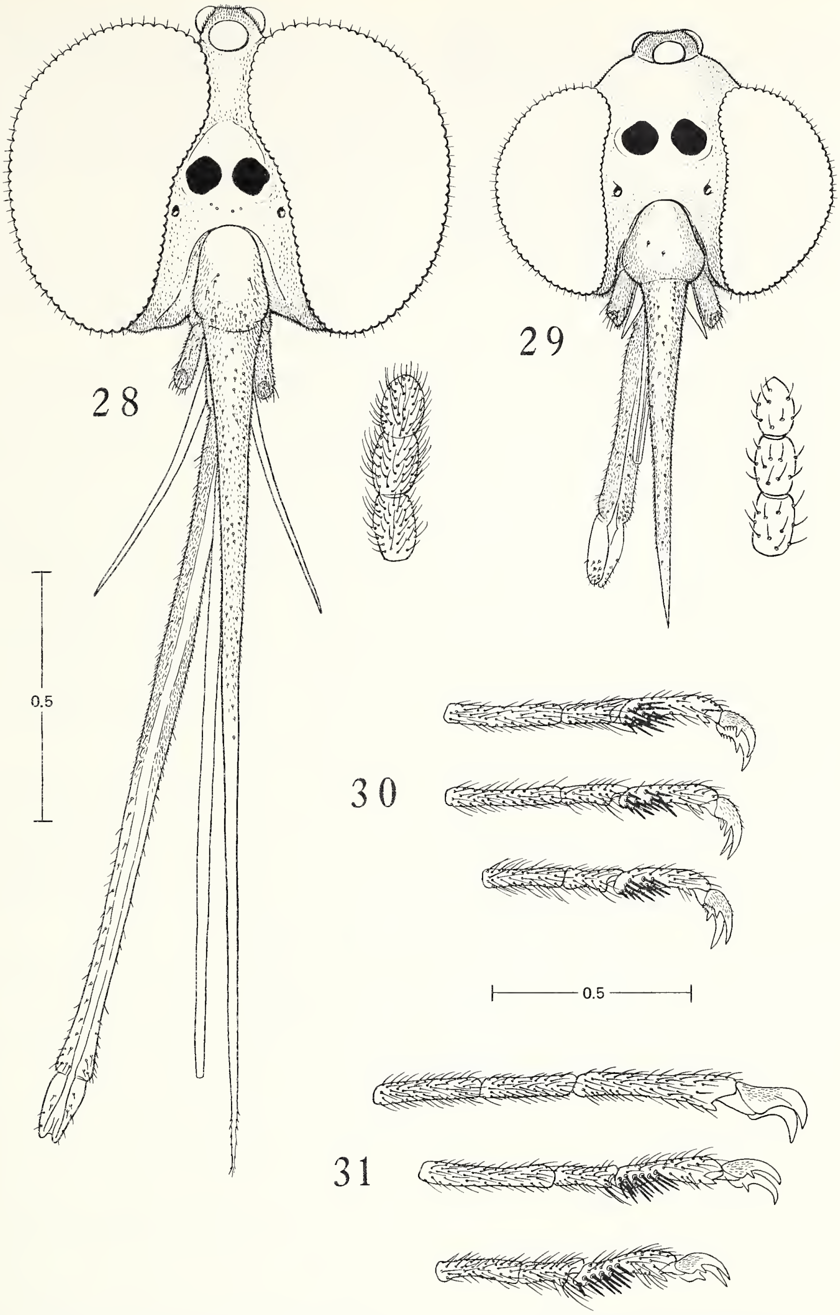
**DESCRIPTION. Male** (Figs. 9–12, 28–31). Only pharate specimens are available (dissected from pupae). *Coloration.* Not available. *Size.* Apparently a medium-sized blephariceridd. Measurements (N = 2) (femur–tarsus 1 unextended and not measurable):

| | | fore leg |
|---|---|---|
| tarsus | 2 | 0.50 |
| | 3 | 0.31 (0.30–0.31) |
| | 4 | 0.18 (0.18–0.18) |
| | 5 | 0.27 (0.26–0.28) |

| | | mid leg |
|---|---|---|
| tarsus | 2 | 0.50 (0.50–0.50) |
| | 3 | 0.32 (0.30–0.34) |
| | 4 | 0.18 (0.17–0.20) |
| | 5 | 0.26 (0.24–0.28) |

| | | hind leg |
|---|---|---|
| tarsus | 2 | 0.38 (0.38–0.38) |
| | 3 | 0.21 (0.21–0.21) |
| | 4 | 0.15 (0.15–0.15) |
| | 5 | 0.23 (0.23–0.24) |

*Head* (Fig. 28). Normal type, subholoptic. Eyes approximate dorsally, interocular distance equal to combined diameters of 3–5 ommatidia; anterior margin of eye smoothly rounded. Mouthparts well developed, proboscis very long, labium about 1.9



Figures 28–31. *Paltostoma aspergonympha.* **28.** Male head (frontal view) and terminal antennal segments (inset). **29.** Female head and terminal antennal segments (arrangement as for male). **30.** Terminal tarsal segments of male (fore leg, upper; mid leg, center; hind leg, lower; lateral view). **31.** Terminal tarsal segments of female (arrangement as for male).

head width; palpus very short, a single elongate segment clearly evident (=segment 3), sensory pit present, large; a basal segment partly developed, 0.2 length of segment 3. Antenna 15-segmented, flagellar segments subcylindrical; ultimate segment slightly shorter (0.9) than penultimate, proportions of apical three segments 1.0–1.0–0.9.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals numerous; occipitals numerous; genals and postgenals absent; labrals numerous, scattered, on basal half only; labials and labellars numerous, scattered throughout.

*Thorax and appendages* (Fig. 30). Anal angle of wing slightly convex, not lobular. Legs long and slender, hind legs stouter than others. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg n.a.–n.a.–n.a.–n.a.–0.6–1.5; mid leg n.a.–n.a.–n.a.–0.6–0.6–1.4; hind leg n.a.–n.a.–n.a.–0.6–0.7–

1.5; tarsomere 3 of fore and mid leg somewhat longer in relation to 4 (1.7) than in hind legs (1.4). Tarsomeres 5 similar on all legs, curved, with pollex of heavy setae; claw sickle-shaped, with sub-basal tooth and trichiate basally.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals, dorsocentrals, supraalars, and prescutellars absent; scutellars very numerous, long and concentrated in a lateral group, a few scattered mediad; preepisternals few (2–3), far ventral; metapleurals few (5–6); suprametapleurals few (4–5).

*Terminalia* (Figs. 9–12). Cerci slightly divergent; interlobular depression shallow, broadly V-shaped; individual cercus broadly triangular. Walls of subanal pouch thin. Apex of tegumen with recurved keel dorsally. Outer gonostylus large, a subrectangular lobe, apicoventral angle expanded, a shallow, elongate groove along ental face. Inner gonostylus elongate, erect, digitiform (apex slightly angled). Expanded bases of aedeagal rods with internal spinules. Lateral rod leaving sperm sac more or less posteriorly and with an arcuate curvature. Lateral tine attenuate, with dense small spines along inner margin of distal half to near tip.

Sensilla.—Epandrium with a few setiforms in medial and lateral groups. Cercus with medium setiforms primarily along posterior margin; setae of inner arm grouped near apex. Outer gonostylus with medium setiforms generally distributed ectally; mixed medium setiforms generally distributed along ventral third of ental surface; expanded ventral lobe non-setate. Alveoliform sensilla of Xth tergite not apparent. Xth sternite with two long setiforms apically.

**Female** (Figs. 14, 29, 31). Only pharate specimens are available (dissected from pupae). *Coloration.* Not available. *Size.* Apparently a medium-sized blephariceri. Measurements (some not available) (N = 2) (femur–tarsus 1 unextended and not measurable):

| | | fore leg |
|---|---|---|
| tarsus | 2 | 0.40 (0.39–0.42) |
| | 3 | 0.27 (0.27–0.27) |
| | 4 | 0.24 (0.23–0.24) |
| | 5 | 0.43 (0.42–0.43) |

| | | mid leg |
|---|---|---|
| tarsus | 2 | 0.58 (0.57–0.59) |
| | 3 | 0.33 (0.32–0.34) |
| | 4 | 0.17 (0.16–0.17) |
| | 5 | 0.27 (0.27–0.27) |

| | | hind leg |
|---|---|---|
| tarsus | 2 | 0.43 (0.43–0.43) |
| | 3 | 0.25 (0.24–0.25) |
| | 4 | 0.16 (0.16–0.16) |
| | 5 | 0.25 (0.24–0.25) |

*Head* (Fig. 29). Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance equal to 0.3 width of head capsule. Mouthparts well developed, mandibles absent, lacinia very short; proboscis moderately long, labium about 1.0 head width; margin of hypopharynx entire; apex of labrum acuminate; palpus very short, a single diminutive segment; sensory pit present. Antenna 15-segmented, flagellar segments barrel-shaped, ultimate subequal to penultimate, proportions of apical three segments 1.0–1.0–0.9.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few, small occipitals few (2–3); postgenals absent; labrals few, scattered, small; labials and labellars numerous, small, scattered throughout.

*Thorax and appendages* (Fig. 31). Anal angle of wing slightly convex, not lobular. Legs long and slender, hind legs slightly less stout than fore legs. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg n.a.–n.a.–n.a.–0.7–0.9–1.8; mid leg n.a.–n.a.–n.a.–0.6–0.5–1.6; hind leg n.a.–n.a.–n.a.–0.6–0.6–1.6; tarsomere 4 of fore leg much longer in relation to 3 (0.9) than in mid and hind legs (0.5–0.6). Fore tarsus longer and stouter than other tarsi, fore tarsomere 5 straight, expanded distad, and without pollex; mid and hind tarsomeres 5 with pollex of several heavy setae; fore claws dissimilar to others, simple, stout hooks, mid and hind claws similar but with small sub-basal tooth, non-trichiate.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals, dorsocentrals, supraalars, and prescutellars absent; scutellars very numerous, long and concentrated in an elongate, brushlike group laterally, none medially; preepisternals indeterminable; metapleurals few (4–5); suprametapleurals few (2–5).

*Terminalia* (Fig. 14). VIIIth sternite well sclerotized throughout, base narrowed; lateral margin curved strongly, medial depression very deep, narrowly V-shaped, internal sclerotization keeled, broad and irregular, lobe incurved, apex closely appressed to hypogynial plate. Hypogynial plate complex, base much broader than lobes; lobe with narrowed neck, dorsal division short, lobulate, nude, ventral division with weak denticulae apically. Spermathecae three, large, weakly sclerotized, all similar, elongate oviform, necks very short and straight.

Sensilla.—Sternite VIII with 5–6 (up to 10 rarely) medium setiforms, restricted to center of lobe.

**Pupa** (Figs. 20–22). *Integument.* Periphery abrupt, ventral sclerotized border developed on thorax only. Papillose dorsally. Papillae even and moderately dense generally. Individual papillae minutely multispinulate (abdomen) to spiniform (branchial sclerite); very small on scutum, larger on branchial sclerite, and largest on abdomen. Papillar distribution as follows: scutum—sparse and few on disc; branchial sclerite—general over entire surface (few centrally); metathoracic and abdominal tergite I—moderately dense, sparser mediad; abdominal tergites II–VIII—even and dense over entire dorsum.

*Size.* Small for family. Measurements, male (N = 10): length 4.0 (3.7–4.5), width 2.1 (1.9–2.5); fe-

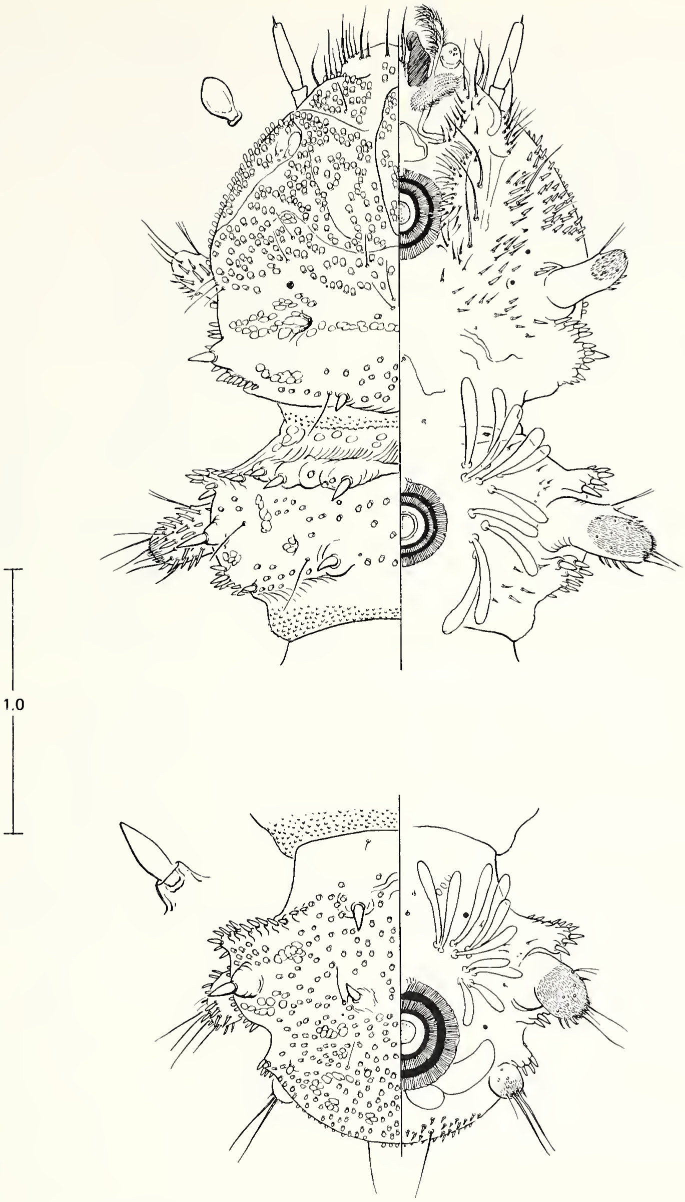


**Figure 32.** *Paltostoma aspergonympha,* larva (dorsal view, left; ventral view, right; typical modified sensilla, insets).

male (N = 10): length 4.3 (4.2–4.6), width 2.3 (2.1–2.5). Male 0.9 size of female.

*General.* Outline shape elliptical, entire (thorax not abruptly narrowed). L/W male = 2.0, female 1.9. Shape in cross section subtriangular (rounded angles; equilateral), sides steeply inclined. Dorsal sclerites: branchial sclerite taller than long, simple, smoothly rounded (no convexities). Anterior margin of scutum gradually inclined. Suture separating metathoracic sclerite from abdominal tergite I, smoothly curved medially. Abdominal tergites smoothly convex middorsally (no medial ridges or nodes); lateral margins entire.

*Branchiae.* Erect, parallel, except hind pair contiguous apically. Outer plates triangular, with acute apices; inner two plates smaller, thinner and narrower than outers; anterior plate largest.

**Larva** (Figs. 25, 32). *General.* Body form subonisciform. Medial elevated zones of abdominal segments well developed. Outline shape of anterior division subovate.

*Integument.* Dorsum well sclerotized. Corrugations very strong, irregular, convergent over circumlateral ridges. Venter with area around bases of pseudopods very finely strigulate, a few scattered setae anterior and posterior to base of each pseudopod.

*Coloration.* Trunk pigmentation even, dark brown; sclerotized portions black; terminal border unpigmented.

*Size.* Medium for genus. Measurements (N = 10): body length 5.9 (5.4–6.4), head capsule width 1.3 (1.1–1.5), antennal segment lengths, basal 0.05 (0.05–0.05), apical 0.22 (0.20–0.24).

*Head.* Distal antennal segment curved at base. Antennal segment proportions 1.0–4.4.

*Trunk.* Dorsum with irregular transverse anterior convexity (including AT tubercle); PT and LT tubercles present. Numerous small circular plates on anal division.

*Anal division.* Dorsal pseudopod small, a nub, directed posterolaterad. Terminal incision not developed. Terminal lobe with convex, broadly rounded posterior margin.

*Primary sensilla* (medium setiforms unless otherwise described). tM–T in line, in close cluster; tI–VI large, modified coniform (similar to modified sensilla on AT convexity and outer tpI–VI). Inner tpP anterior to spiracle. Outer tpI–VI represented by large, modified, coniform sensilla (similar to modified sensilla on AT convexity and tI–VI). Terminal setae 1–1, widely separated.

*Dorsal modified sensilla.* Large oviforms in linear series and patches on head sclerites and prothorax. Scattered ellipsoid sensilla on I–VIII; these more numerous and denser on terminal division. Transverse anterodorsal convexities on II–VI each bearing a conspicuous heavy coniform seta (similar to tI–VI and outer tpI–VI), giving way laterally to a linear series of similar but increasingly smaller setae, series curving ventrad around base of pseudopod. Background field of fine setiforms absent.

**SPECIMENS EXAMINED.** Types: HOLOTYPE male (dissected from pupa and mounted on slides nos. CLH 86-541, 86-615, and 88-73); ALLOTYPE female (dissected from pupa and mounted on slides nos. CLH 86-626, 86-627, and 87-209; 5 male and 4 female PARATYPES (all pharate adults in pupal cases, terminalia and heads dissected from pupae and mounted on slides): COLOMBIA, *Antioquia,* Quebrada El Treinta & nearby stream, 2 km N Palmitas, 22 Jun 1983, C.L. Hogue, CLH 302, 303 (LACM).

**Additional Specimens.** COLOMBIA, *Antioquia,* same data as types (46 larvae, 69 pupae). No specific locality, Aug 1983, I. Bedoya 2 (6 larvae); 1 km SE Paso de Boquerón, 22 Jun 1983, C.L. Hogue, CLH 300 (1 larva).

**ETYMOLOGY.** The name is a compound noun meaning "spray sprite" (Latin: *aspergo* = spray + *nympha* = water sprite).

**REMARKS.** Association of the stages is certain: larva–pupa–adults by the ontogenetic method.

## 3. *Paltostoma charadrae* Hogue, new species

Figures 15, 26, 33–40, 45, 53

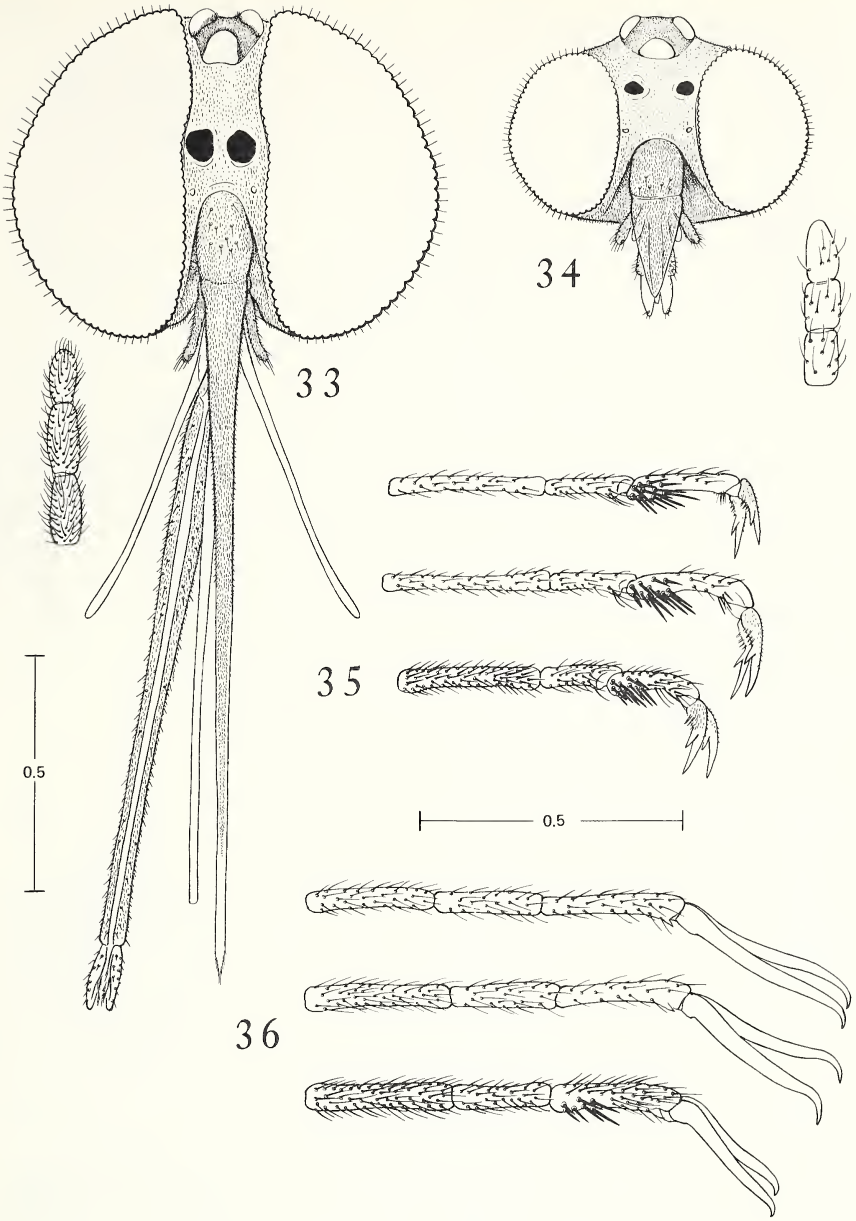
**DIAGNOSIS.** *Adult.*—Adults have a single palpal segment like *roldani* and *eldorado,* but the ultimate antennal segment is slightly shorter, rather than much longer, than the penultimate as in those species. In the male terminalia, the lateral tine is uniquely unspined; the female terminalia are like those of *eldorado,* i.e., with a broad median depression between the VIIIth sternite lobes and with microtrichiae on the ventral thumblike lobe of the hypogynial plate. However, the internal sclerotization at the base of the medial depression is lanceolate rather than subquadrate in outline. *Pupa.*—The pupae of *charadrae* and *eldorado* are very similar and difficult to distinguish. The best separation is by the shape and arrangement of the branchial lamellae: in *charadrae* the outer plates are somewhat contorted and acuminate apically; the anterior plate is apically twisted upward so that, in dorsal aspect, the opposite plates are parallel and the apices of the posterior plates are contiguous; in *eldorado* the outer plates are straight, the anterior plates divergent and the apices of the posterior plates are only approximate. *Larva.*—This stage is identified by the narrowed terminal lobe, spiniform setae posteriad only on the pseudopods, and poorly developed circumlateral series of dorsal modified setae.

**DESCRIPTION. Male** (Figs. 33, 35). *Coloration.* Ground color velvety, blackish-brown, darker and tending toward black on anterior portion of scutum. Head, thorax, and abdomen with silvery pollinosity, forming irregularly appearing and disappearing patches as specimen is rotated in light from certain angles. Legs very dark, almost black, dull, without evident pollinosity. Wing membrane infuscate. *Size.* A small blephariceridd. Measurements (N = 10): wing length 4.4 (4.1–4.7). Leg segment lengths:

| | | fore leg |
|---|---|---|
| femur | | 2.0 (1.9–2.3) |
| tibia | | 2.3 (2.1–2.6) |
| tarsus | 1 | 1.4 (1.6–1.2) |
| | 2 | 0.49 (0.45–0.55) |
| | 3 | 0.30 (0.26–0.34) |
| | 4 | 0.15 (0.13–0.18) |
| | 5 | 0.22 (0.20–0.24) |

| | | mid leg |
|---|---|---|
| femur | | 2.8 (2.5–3.2) |
| tibia | | 2.4 (2.2–2.7) |
| tarsus | 1 | 1.2 (1.1–1.4) |
| | 2 | 0.47 (0.42–0.54) |
| | 3 | 0.28 (0.18–0.32) |
| | 4 | 0.15 (0.13–0.16) |
| | 5 | 0.23 (0.21–0.25) |

| | | hind leg |
|---|---|---|
| femur | | 3.5 (3.2–3.9) |
| tibia | | 3.5 (3.2–4.0) |
| tarsus | 1 | 1.3 (1.2–1.5) |
| | 2 | 0.46 (0.40–0.53) |
| | 3 | 0.27 (0.23–0.31) |
| | 4 | 0.16 (0.15–0.18) |
| | 5 | 0.21 (0.18–0.24) |

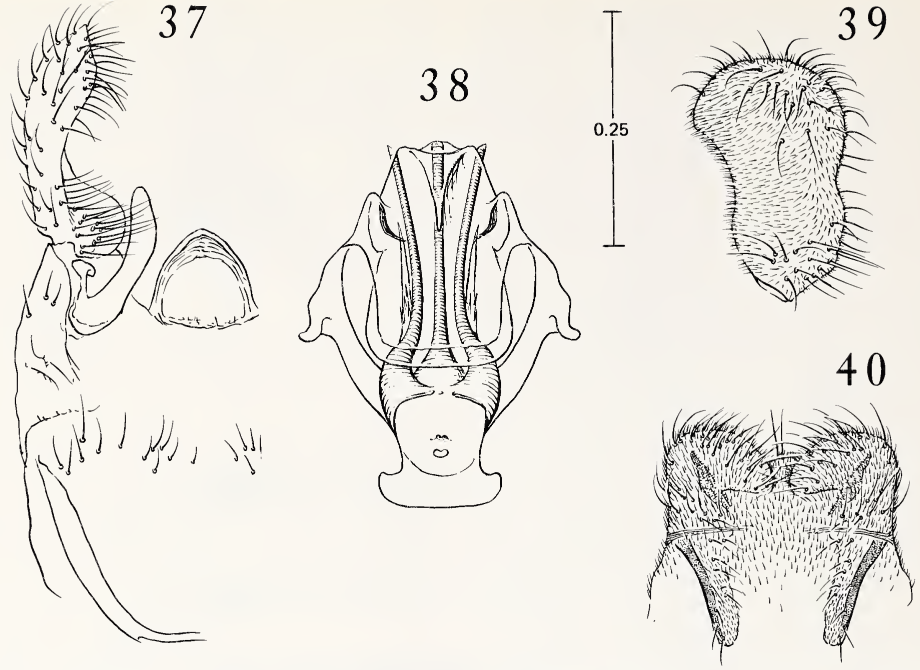


**Figures 33–36.** *Paltostoma charadrae.* **33.** Male head (frontal view) and terminal antennal segments (inset). **34.** Female head and terminal antennal segments (arrangement as for male). **35.** Terminal tarsal segments of male (fore leg, upper; mid leg, center; hind leg, lower; lateral view). **36.** Terminal tarsal segments of female (arrangement as for male).

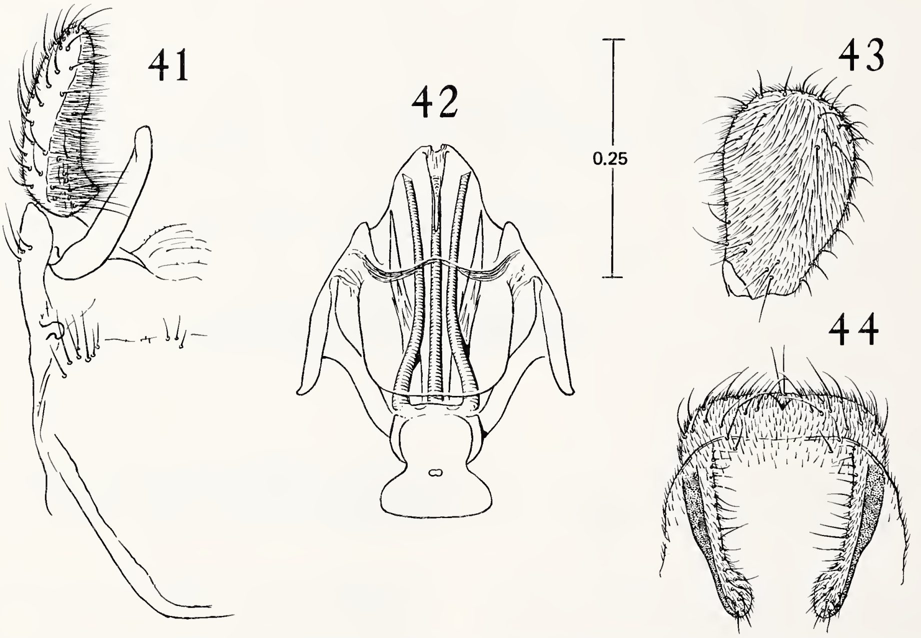
*Head* (Fig. 33). Normal type, subholoptic. Eyes disjunct dorsally, interocular distance about 0.2 head width; anterior eye margin sharply excised to accommodate antennal sockets. Mouthparts well developed, proboscis long, labium about 1.7 head width; palpus very short, a single elongate segment clearly evident (=segment 3), sensory pit vestigial; a basal segment partly developed, 0.25 length of segment 3. Antenna 15-segmented, flagellar segments elongate barrel-shaped; ultimate segment smaller than (0.8) penultimate, proportions of apical three segments 1.0–1.0–0.8.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals several (9–12); occipitals few (2–3); postgenals few (5); labrals absent; labials and labellars numerous, scattered throughout.

*Thorax and appendages* (Fig. 35). Anal angle of wing produced, lobular. Legs long and slender, hind leg stouter than others. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg 1.1–0.6–0.4–0.6–0.5–1.4; mid leg 0.9–0.5–0.4–0.6–0.5–1.6; hind leg 1.0–0.4–0.4–0.6–0.6–1.3; tarsomere 4 short in relation to 3 in all legs (0.5–0.6). Tarsomeres 5



**Figures 37–40.** *Paltostoma charadrae,* male terminalia (dorsal views). **37.** Genital capsule and gonostyli. **38.** Mesosomal structures and gonites. **39.** Left outer gonostylus (inner view). **40.** Cercal complex.



**Figures 41–44.** *Paltostoma eldorado,* male terminalia (dorsal views). **41.** Genital capsule and gonostyli. **42.** Mesosomal structures and gonites. **43.** Left outer gonostylus (inner view). **44.** Cercal complex.

similar on all legs, curved, with pollex of heavy setae; claw sickle-shaped, with sub-basal tooth and trichiate basally, several heavy trichiae ventrally between base and tooth.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; dorsocentrals few (2), posterior; supraalars and prescutellars absent; scutellars numerous, in lateral group, a few setae scattered mediad; preepisternals absent; metapleurals numerous (13); suprametapleurals few (3).

*Terminalia* (Figs. 37–40). Cerci parallel; interlobular depression shallow, V-shaped; individual cercus broadly rounded. Walls of subanal pouch thin. Apex of tegmen with medial recurved keel dorsally. Outer gonostylus large, an obovate lobe, apicodorsal angle slightly produced. Inner gonostylus elongate, erect, digitiform (apex simple). Expanded bases of aedeagal rods lacking internal spinules. Lateral rod leaving sperm sac laterally, base arcuate. Lateral tine attenuate, short, with small spines sub-basally.

Sensilla.—Epandrium with a few medium setiforms in a sparse transverse series. Cercus with a few medium setiforms scattered on apicodorsal third and basally; setae of inner arm few and evenly dispersed along entire length. Outer gonostylus with medium setiforms general ectally; sparse basal and apical groups entally. Alveoliform sensilla of Xth tergite not apparent. Xth sternite with two long setiforms apically.

**Female** (Figs. 34, 36). A single pharate specimen is available (dissected from pupa and mounted on slide). *Coloration.* As in male. Wing membrane infuscate. *Size.* A medium-sized blephariceric. Measurements (N = 1): wing length 6.2. Leg segment lengths (femur–tarsus 1 unextended and not measurable):

| | | fore leg | mid leg | hind leg |
|---|---|---|---|---|
| tarsus | 2 | 0.38 | 0.38 | 0.49 |
| | 3 | 0.29 | 0.27 | 0.28 |
| | 4 | 0.21 | 0.21 | 0.19 |
| | 5 | 0.27 | 0.27 | 0.24 |

*Head* (Fig. 34). Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance equal to 0.3 width of head capsule. Mouthparts poorly developed, mandibles absent, lacinia very short; proboscis very short, labium about 0.28 width of head capsule; margin of hypopharynx entire; apex of labrum rounded; labellar lobes straight, shorter than base of labium; palpus very short, a single diminutive segment (=segment 3), sensory pit absent. Antenna 15-segmented, flagellar segments elongate cylindrical, ultimate segment equal to penultimate, proportions of apical three segments 1.0–1.0–1.0.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few (5), scattered, small; occipitals few (5); postgenals absent; labrals absent; labials several, scattered generally, labellars few, small, restricted to apex.

*Thorax and appendages* (Fig. 36). Anal angle of wing produced, lobular. Legs moderately long and slender; hind legs stouter than others. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg n.a.–n.a.–n.a.–0.8–0.7–1.3; mid leg n.a.–n.a.–n.a.–0.7–1.0–1.3; hind leg n.a.–n.a.–n.a.–0.6–0.7–1.3; tarsomere 4 short in relation to 3 on all legs (0.7). Fore and mid tarsomeres 5 similar, straight, without pollex; hind tarsomere 5 curved, with weak pollex of enlarged setae; claw simple, long, slender, and gently sigmoidally curved, non-trichiate; hind claw somewhat stouter and shorter than others.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals, dorsocentrals, supraalars, and prescutellars absent; scutellars very numerous, long and concentrated in an elongate, brushlike group laterally, a few scattered mediad; preepisternals absent; metapleurals several (6); suprametapleurals few (3).

*Terminalia* (Fig. 15). VIIIth sternite well sclerotized throughout, base broad; lateral margin straight, medial depression moderately deep, broadly V-shaped, internal sclerotization flat, fusiform; lobe straight, apex not closely appressed to hypogynial plate. Hypogynial plate complex, base as broad as lobes, lobe with broad necks, dorsal division short, lobulate, nude, ventral division microtrichiate laterally, becoming denticulate mediad. Spermathecae three, all large, weakly sclerotized, two similar, elongate oviform, third about two-thirds size of others, oviform; necks very short and straight.

Sensilla.—Sternite VIII with 18–23 medium setiforms, distributed generally over lobe.

**Pupa** (Fig. 45). Very similar to pupa of *P. eldorado. Integument.* Periphery rounded, sclerotized integument underfolded and forming broad ventral border all around. Papillose dorsally. Papillae even and very dense generally (individual papillae nearly contiguous). Individual papillae small, those of scutum slightly larger than others; smooth, rounded, oval convexities. Papillar distribution as follows: scutum—dense over entire disc; branchial sclerite—dense over entire surface; metathoracic and abdominal tergites—even and dense over entire dorsum.

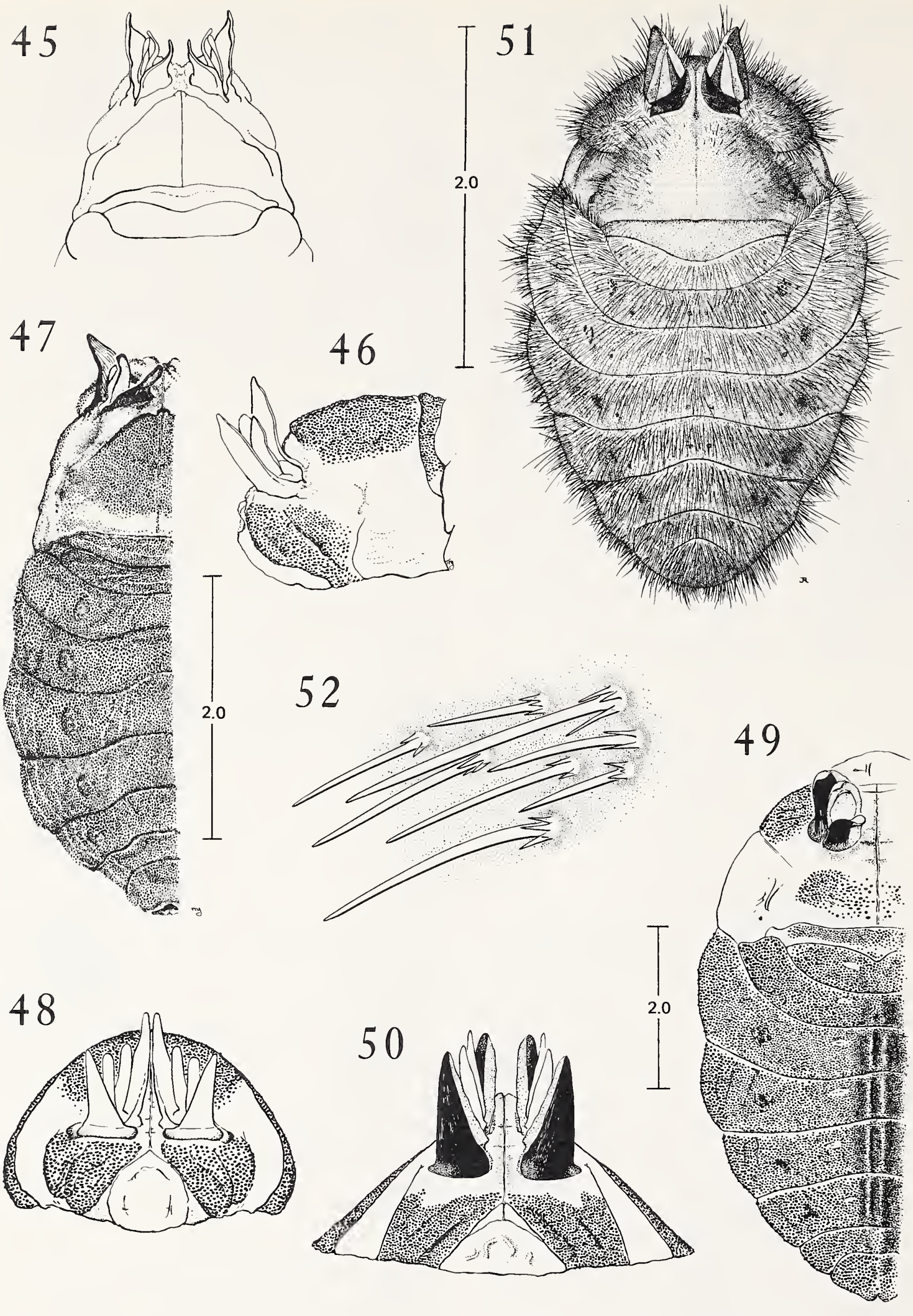
*Size.* Small for family. Measurements, male (N = 10): body length 3.7 (3.6–4.0), width 2.0 (1.8–2.2); female (N = 10): body length 3.7 (3.0–4.2), width 2.0 (1.8–2.3). Male 1.0 size of female.

*General.* Outline shape elliptical, entire (thorax not abruptly narrowed). L/W male = 1.9, female 1.9. Shape in cross section subtriangular (angles rounded, equilateral), sides steeply inclined. Dorsal sclerites: cephalic sclerite with slight bosses submedially. Branchial sclerite longer than tall, slightly protuberant anteriad in male, not so in female (as viewed from above); with a shallow concavity centrally. Anterior margin of scutum steep but not sharply precipitous, not lobed. Suture separating metathoracic sclerite from abdominal tergite I smooth medially. Abdominal tergites smoothly convex middorsally (no medial ridges or nodes); lateral margins entire.

*Branchiae.* Porrect, anterior plates divergent, middle parallel, hind approximate apically.

Larva (Figs. 26, 53). Similar to *P. eldorado. General.* Body form subonisciform. Medial elevated zones of abdominal segments well developed. Integument of anterior and posterior depressed zones faintly coriaceous. Outline shape of anterior division subovate.

*Integument.* Dorsum moderately well sclerotized. Corrugations distinct, irregular to linear; linear corrugations convergent over anterior and pos-



**Figures 45–52.** *Paltostoma,* pupae. **45.** *P. charadrae,* anterior portion, dorsal view. **46.** *P. eldorado,* anterior portion, lateral view. **47.** Same, left half, dorsal view. **48.** Same, frontal view. **49.** *P. inca,* left half, dorsal view. **50.** Same, frontal view. **51.** *P. andeana,* entire, dorsal view. **52.** Same, details of cuticular bristles.

terior transverse ridges. Venter with area at bases of pseudopods with blunt denticulae.

*Coloration.* Trunk pigmentation even, light brown; sclerotized portions pale brown, terminal border unpigmented.

*Size.* Medium for the family. Measurements (N = 3): body length 5.8 (5.7–6.1), head capsule width 1.1 (1.0–1.2), antennal segment lengths, basal 0.05 (0.05–0.05), apical 0.13 (0.13–0.14).

*Head.* Antennal segment proportions 1.0–2.7.

*Trunk.* Dorsum of abdominal segments I–VI more or less evenly rounded, without convexities or projections; numerous small plates on anal division.

*Anal division.* Dorsal pseudopod small, a nub, directed posterolaterad. Terminal incision not developed. Terminal lobe narrowed posteriad, with convex posterior margin.

*Primary sensilla* (medium setiforms unless oth-

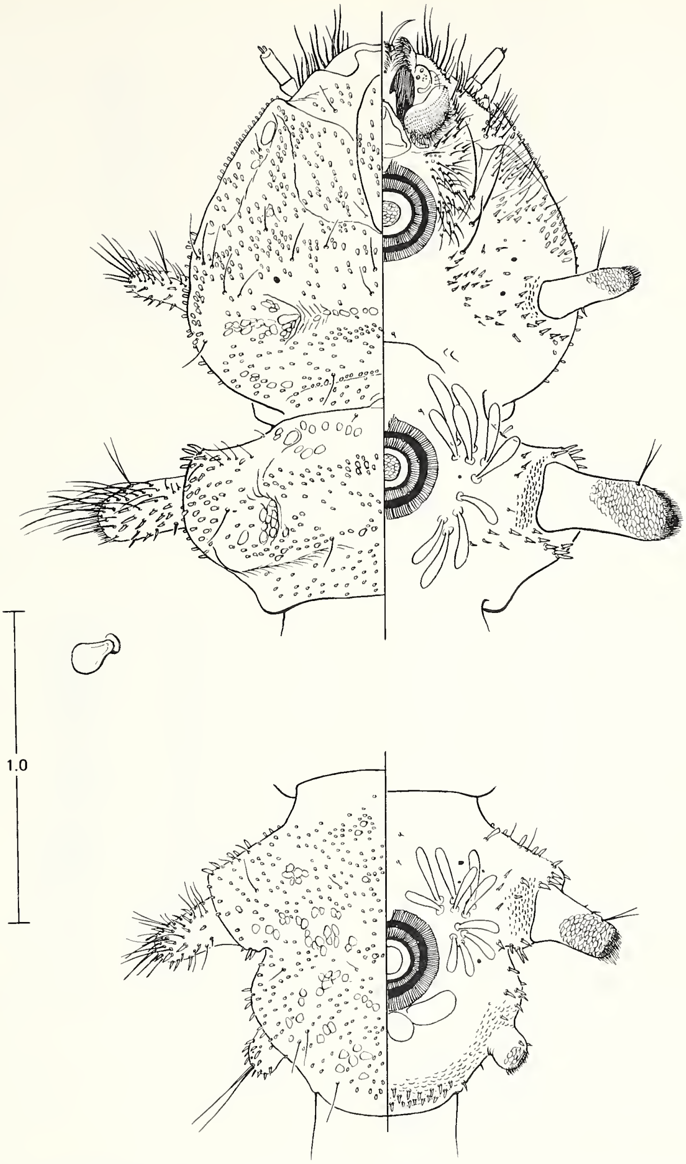


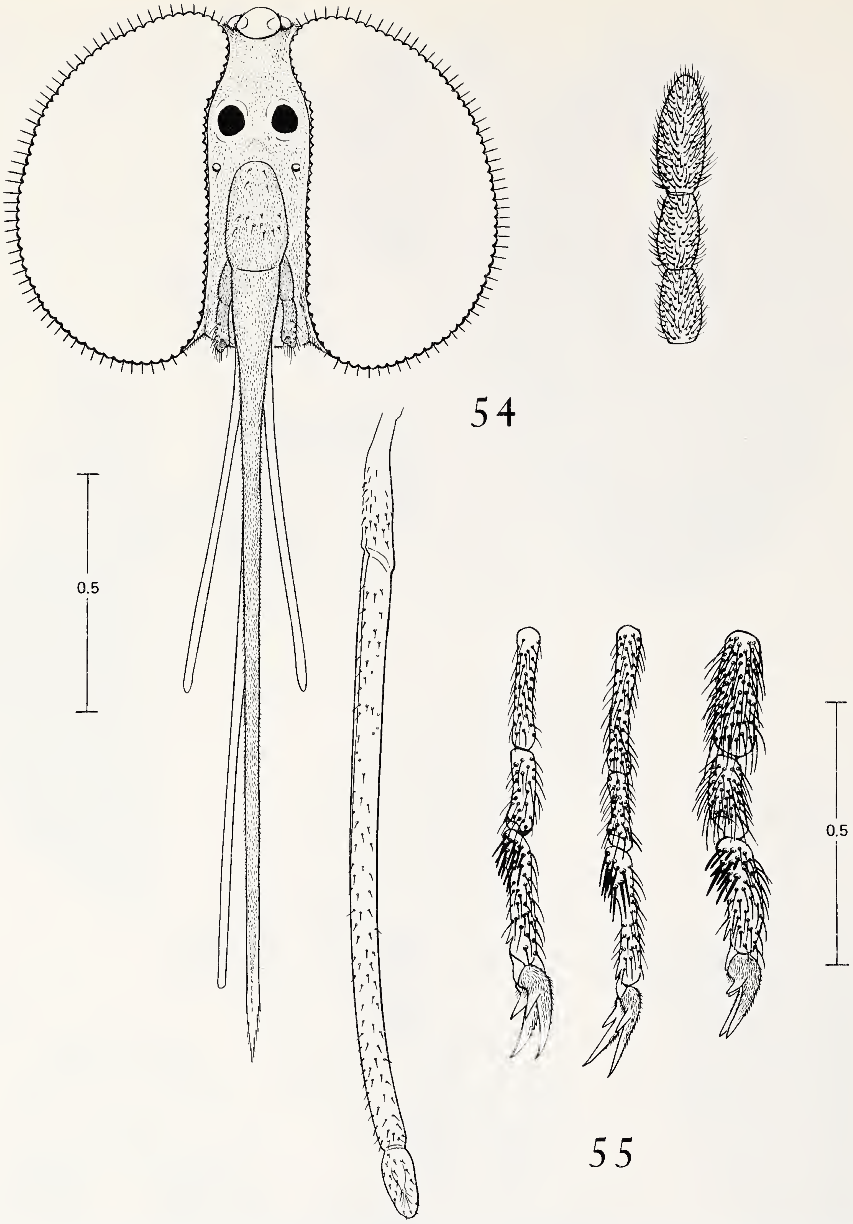
**Figure 53.** *Paltostoma charadrae,* larva (dorsal view, left; ventral view, right; typical modified sensillum, inset).

erwise described). tM–T oblique, tM slightly more medial. stM–T indiscernible; stI–VI distant from tI–VI, tI–VI small, ovoid, sessile (no PT tubercle). stVII and inner tp proximate. Inner tpP anterolateral to spiracle; inner tpI–VI set well anteriad. Outer tpI–VI indiscernible. Terminal setae 1–1, widely separated.

*Dorsal modified sensilla.* Small pyriforms/oviforms in linear series and patches on head sclerites, small pyriforms general on body integument, somewhat clustered in AT and PT areas. Circumlateral series complete. Sensilla of pseudopods setiform anteriorly; posteriorly acute to lanciform. Background field of fine setiforms absent.

**SPECIMENS EXAMINED.** Types: HOLOTYPE male (terminalia on slide no. CLH 87-114); ALLOTYPE female (dissected from pupa and mounted on slides nos. CLH 88-3B, 88-3W, 88-3H, and 86-577); 23 male PARATYPES (one dissected from pupa): COLOMBIA, *Antioquia,* 1 km SE Paso de Boquerón, 22 Jun 1983, C.L. Hogue, CLH 300 (LACM).

**Additional Specimens.** COLOMBIA, *Antioquia,* same data as types (12 larvae, 17 pupae). No specific data, Aug 1983, I. Bedoya 5 (6 larvae). 12 km W Piedra Blanca, Guarne, 8 Jan 1986, C.L. Hogue, CLH 347.1.2 (1 larva, 3 pupae). Quebrada La Cascada, 9.1 km E Medellín, 23 Jun 1983, C.L. Hogue,



**Figures 54, 55.** *Paltostoma eldorado.* **54.** Male head (frontal view) and terminal antennae segments (inset). **55.** Terminal tarsal segments of male (fore leg, left; mid leg, center; hind leg, right; lateral view).

CLH 309.1 (5 larvae, 6 pupae). Quebrada El Treinta, 2 km N Palmitas, 22 Jun 1983, C.L. Hogue, CLH 303 (1 pupa).

*Quindio,* Quebrada Salado, 4 km E Calarcá, 20 Jun 1984, C.L. Hogue, CLH 338 (2 females, 2 larvae, 28 pupae).

**ETYMOLOGY.** The name is a noun in the genitive case transliterated from Greek (*charadra* = rocky gorge), referring to the "bed of a mountain torrent." In like terrain the species is found.

**REMARKS.** Association of pupa-adults is by the ontogenetic method, of larva-pupa by syntopy. The species appears to be very closely related to *P. eldorado.*

## 4. *Paltostoma eldorado* Hogue, new species

Figures 27, 41–44, 46–48, 54–56

**DIAGNOSIS.** *Adult.*—By external characters, the adults of this species are indistinguishable from those of *P. roldani* (both with a single palpal segment and ultimate antennal segment longer than penultimate). In the male terminalia the outer aedeagal rods arise abruptly from the posterolateral corners of the sperm sac and are more or less straight; also the outline shape of the outer gonostylus is simple, without lobes of any kind. In the female terminalia the species is like *charadrae,* i.e., with a broad median depression between the VIIIth sternite lobes and with microtrichiae on the inner thumblike lobe of the hypogynial plate, but the sclerotization at the base of the medial depression is lanceolate rather than subquadrate in outline. *Pupa.*—The pupa of *eldorado* is very similar and difficult to distinguish from that of *charadrae.* The best separation is by the shape and arrangement of the branchial lamellae: in *eldorado* the outer plates are straight, the anterior plates divergent; the apices of the posterior plates are approximate only; in *charadrae* the outer plates are somewhat contorted and acuminate apically; the anterior plate is apically twisted upward so that, in dorsal aspect, the opposite plates are parallel; the apices of the posterior plates are contiguous. *Larva.*—The larva is most similar to that of *P. saltana,* both with a short basal antennal segment and homogeneous dorsal secondary setae, but the pleural margin of the abdominal segment VII is entire anterior to the dorsal pseudopod rather than excised as in that species.

**DESCRIPTION. Male** (Figs. 41–44, 54, 55). Only pharate specimens are available (dissected from pupae). *Coloration.* Not available. *Size.* A small blephariceríd. Measurements from a single pharate specimen, dissected from pupa and mounted on slide: wing length indeterminable. Leg segment lengths as follows (femur–tarsus 1 unextended and not measurable):

| | | fore leg | mid leg | hind leg |
|---|---|---|---|---|
| tarsus | 2 | 0.54 | 0.49 | 0.41 |
| | 3 | 0.29 | 0.30 | 0.24 |
| | 4 | 0.19 | 0.16 | 0.16 |
| | 5 | 0.25 | 0.29 | 0.23 |

*Head* (Fig. 54). Normal type, subholoptic. Eyes disjunct dorsally, anterior eye margin sharply incised to accommodate antennal sockets, interocular distance about 0.2 head width. Mouthparts well developed, proboscis long, labium about 1.5 head width; palpus short, a single elongate segment clearly evident (=segment 3), sensory pit present; a basal segment partly developed, length 0.6 segment 3. Antenna 15-segmented, flagellar segments elongate barrel-shaped, ultimate segment longer (1.5) than penultimate, proportions of apical three segments 1.0–1.0–1.5.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals numerous (12–16), scattered; occipitals few (3–4); postgenals few (5–6), short; labrals absent; labials and labellars numerous, scattered throughout.

*Thorax and appendages* (Fig. 55). Anal angle of wing produced, lobular. Legs long and slender; hind legs somewhat stouter than other legs. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg n.a.–n.a.–n.a.–0.5–0.7–1.3; mid leg n.a.–n.a.–n.a.–0.6–0.5–1.8; hind leg n.a.–n.a.–n.a.–0.6–0.7–1.4; tarsomere 4 short in relation to 3 in all legs (0.5–0.6). Tarsomeres 5 similar on all legs, curved, with pollex of enlarged setae; pollex of fore and mid legs weak, setae only slightly enlarged, pollex of hind legs well developed with heavy setae; claw sickle-shaped, with sub-basal tooth and trichiate basally, several heavy trichiae ventrally between base and tooth, fore claw slightly heavier than other claws.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals and dorsocentrals absent; supraalars, prescutals (seven setae on anteromedial margin of scutum), and prescutellars absent; scutellars numerous, in lateral group, a few setae scattered mediad; preepisternals few (2); metapleurals several (9–10); suprametapleurals few (4).

*Terminalia* (Figs. 41–44). Cerci parallel; interlobular depression very shallow and small; individual cercus broad, slightly truncate. Walls of subanal pouch thin. Apex of tegmen with recurved keel dorsally. Outer gonostylus moderately large, a simple obovate lobe. Inner gonostylus elongate, erect, digitiform (apex slightly angled). Expanded bases of aedeagal rods lacking internal spinules. Lateral rod leaving sperm sac posteriorly with only a slight curvature. Lateral tine attenuate, with a few small spines midlength.

Sensilla.—Epandrium with a few medium setiforms in a group sublaterally and a few small setiforms medially. Cercus with a few medium setiforms scattered on apicodorsal third; setae of inner arm few and grouped near apex. Outer gonostylus with medium setifoms general ectally; sparse basal and apical groups entally. Alveoliform sensilla of Xth tergite not apparent. Xth sternite with two long setiforms apically.

**Female** (not figured). Only a single, subpharate specimen is available (partly dissected from pupa). *Coloration.* Indeterminable. *Size.* Apparently a medium-sized blepharicerid. Measurements indeterminable.

*Head.* Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance equal to 0.27 width of head capsule. Mouthparts poorly developed; mandibles absent, character states of lacinia and hypopharynx indeterminable; proboscis very short, labial length indeterminable, labrum only about 0.2 width of head capsule; apex of labrum rounded; size of labellar lobes indeterminable, undeveloped on specimen; palpus very short, a single diminutive segment (=segment 3), sensory pit present but vestigial. Antenna 15-segmented, flagellar segments barrel-shaped, ultimate segment equal to penultimate, proportions of apical three segments 1.0–1.0–1.0.

Sensilla.—Setiform groups on head capsule and mouthparts as follows (specimen poor, setal states mostly indeterminable): clypeals absent, scattered, small; occipitals apparently few (4); postgenals few (2); labrals absent; labials and labellars indeterminable.

*Thorax and appendages; terminalia.* Structures undeveloped on specimen; all character states indeterminable.

**Pupa** (Figs. 46–48). Very similar to pupa of *P. charadrae. Integument.* Periphery rounded, scler-

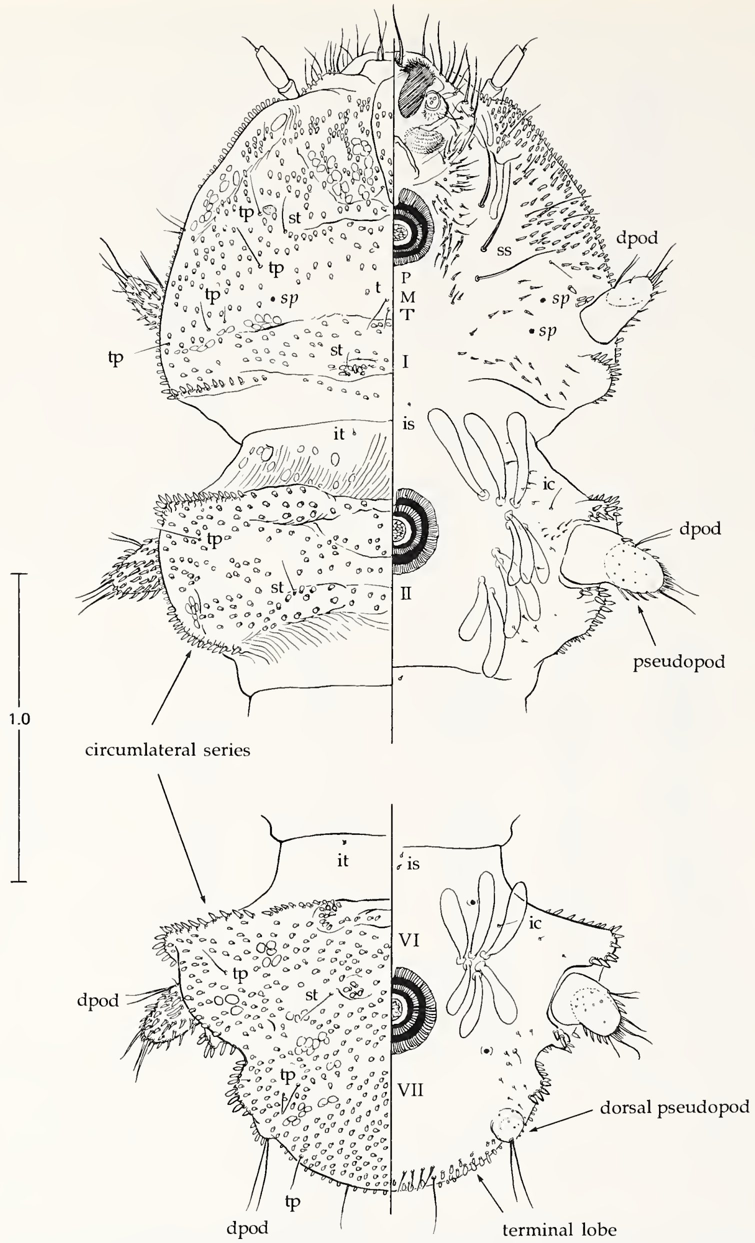


**Figure 56.** *Paltostoma eldorado,* larva (dorsal view, left; ventral view, right); anatomical details labeled: primary sensilla, t—tergal, st—subtergal, tp—tergopleural, dpod—dorsal pseudopodal, it—intertergal, is—intersternal, ic—intercalary, ss—substernal, *sp*—spiracle.

otized integument underfolded and forming broad ventral border all around. Papillose dorsally. Papillae even and very dense generally (individual papillae nearly contiguous). Individual papillae small, those of scutum conspicuously larger than others; smooth, rounded, oval convexities. Papillar distribution as follows: scutum—dense over entire disc; branchial sclerite—dense over entire surface; metathoracic and abdominal tergites—even and dense over entire dorsum.

*Size.* Small for family. Measurements, male (N = 10): body length 4.2 (3.9–4.6), width 2.1 (2.1–2.3); female (N = 8): body length 4.6 (4.4–4.8), width 2.5 (2.3–2.7). Male 0.8 size of female.

*General.* Outline shape elliptical, entire (thorax not abruptly narrowed). L/W male = 2.0, female 1.9. Shape in cross section subtriangular (angles rounded, equilateral), sides steeply inclined. Dorsal sclerites: cephalic sclerite with broad, irregular, inverted U-shaped ridge against upper margin. Branchial sclerite longer than tall, strongly protuberant anteriad in male, barely so in female (as viewed from above), complex in both sexes, with a strong furrow curving obliquely from base of branchiae to posteroventral corner of sclerite. Anterior margin of scutum sharply precipitous, trilobed. Suture separating metathoracic sclerite from abdominal tergite I smoothly rounded medially. Abdominal tergites smoothly convex middorsally (no medial ridges or nodes); lateral margins entire.

*Branchiae.* Porrect, anterior plates divergent, middle parallel, hind contiguous apically.

**Larva** (Figs. 27, 56). *General.* Body form onisciform. Medial elevated zones of abdominal segments well developed. Outline shape of anterior division subovate.

*Integument.* Dorsum moderately well sclerotized. Corrugations distinct, linear to irregular, forming areolate pattern, linear corrugations convergent over anterior and posterior transverse ridges. Integument of anterior and posterior depressed zones faintly coriaceous. Venter with area medial to bases of pseudopods minutely strigulate; minute setae anterior and posterior to base of pseudopod.

*Coloration.* Trunk pigmentation even, light brown; sclerotized portions pale brown, terminal border unpigmented.

*Size.* Medium for the family. Measurements (N = 10): body length 5.8 (5.4–6.2), head capsule width 1.3 (1.2–1.4), antennal segment lengths, basal 0.05 (0.05–0.05), apical 0.17 (0.16–0.19).

*Head.* Antennal segment proportions 1.0–3.5.

*Trunk.* Dorsum of abdominal segments I–VI with anterior and posterior, transverse pillowlike convexities (strongest in AT and PT positions). Numerous small circular plates on anal division.

*Anal division.* Dorsal pseudopod small, a nub, directed posterolaterad. Terminal incision not developed. Terminal lobe with convex, broadly rounded posterior margin.

*Primary sensilla* (medium setiforms unless otherwise described). tM–T small, in line and closely clustered. stM–T close to and lateral to t, small; stI–VI associated with PT convexity. Inner tpP anterolateral to spiracle; inner tpI–VI set well anteriad, outer tpI–VI indiscernible. Terminal setae 1–1, widely separated.

*Dorsal modified sensilla.* Small pyriforms/oviforms in linear series and patches on head sclerites, scattered on trunk segments except for dense groupings on AT and PT convexities. Circumlateral series extensive and complete. Sensilla of pseudopods setiform apically; dorsally acute to lanciform. Background field of fine setiforms absent.

**SPECIMENS EXAMINED.** Types: HOLOTYPE male (ex pupa in alcohol, dissected and mounted on slides nos. CLH 87-215H, 87-215B, 87-215W, and 87-215T); ALLOTYPE female (ex pupa in alcohol, partially on slides nos. CLH 86-519 and 86-520); 3 male PARATYPES (all dissected from pupae, terminalia mounted on slides): COLOMBIA, *Antioquia,* Quebrada Piedra Blanca, 12 km W Guarne, 8 Jan 1986, C.L. Hogue, CLH 347.1.1, 347.1.2 (LACM).

**Additional Specimens.** COLOMBIA, *Antioquia,* same data as types (23 pupae). Salto Tequendamita, 23 Jun 1983, C.L. Hogue, CLH 310 (1 pupa).

*Caldas,* 6 km N Manizales, 17 Jun 1984, C.L. Hogue, CLH 336 (28 larvae).

**ETYMOLOGY.** The species is named in honor of the famed "Golden Man" of Colombian antiquity and his fabled cache of gold, long sought by the Conquistadors but never found. The name is used in the nominative case and in apposition to the generic appelation.

**REMARKS.** Association of the pupa-adult was by the ontogenetic method. No larvae have been collected with known pupae of this species so the larva-pupa association is by the phyletic inference method (larvae and pupae are both very similar to those of *charadrae*).

## 5. ? *Paltostoma saltana* Edwards, 1929

Figures 57, 75

*Paltostoma saltana* Edwards, 1929:71–73, figs. 37, 42, 48, 62–65.

**REDESCRIPTION. Larva** (Figs. 57, 75). *General.* Body form subonisciform. Abdominal segments with medial elevated ridges. Outline shape of anterior division subovate.

*Integument.* Dorsum well sclerotized. Corrugations distinct, mostly linear, convergent across transverse anterior and posterior ridges. Integument of anterior and posterior depressed zones corrugopapillose. Venter with area at bases of pseudopods very finely strigulate, a few scattered setae in area.

*Coloration.* Trunk dark brown, evenly pigmented; sclerotized portions pale brown, terminal border unpigmented.

*Size.* Medium for the family. Measurements (N = 4): body length 8.8 (8.2–9.2), head capsule width 2.1 (1.9–2.3), antennal segment lengths, basal 0.05 (0.05–0.05), apical 0.10 (0.10–0.11).

*Head.* Antennal segment proportions 1.0–2.1.

*Trunk.* Dorsum irregular, especially laterad: circumlateral ridges very prominent, especially anterior; both irregular; strong lateral lobes anterior and posterior to bases of pseudopods of trunk segments and on abdominal segment VII.

*Anal division.* Dorsal pseudopod small, a nub, directed posterolaterad. Terminal incision not developed. Terminal lobe with convex, broadly rounded posterior margin.

*Primary sensilla* (medium setiforms unless otherwise described). tM–T in line, well spaced. stI–VI very small. stVII and inner tp proximate. Inner tpP slightly medial to spiracle. Outer tpI–VI indiscernible. Terminal setae 1–1, widely separated.

*Dorsal modified sensilla.* Of special form: wide, pyriform with flattened apex that is occasionally collapsed, rim minutely denticulate. Slight modifications of these special sensilla in linear series and patches on head sclerites. Circumlateral ridges strong, irregular. Sensilla in circumlateral series uniform in size and shape, glandiform. A similar series

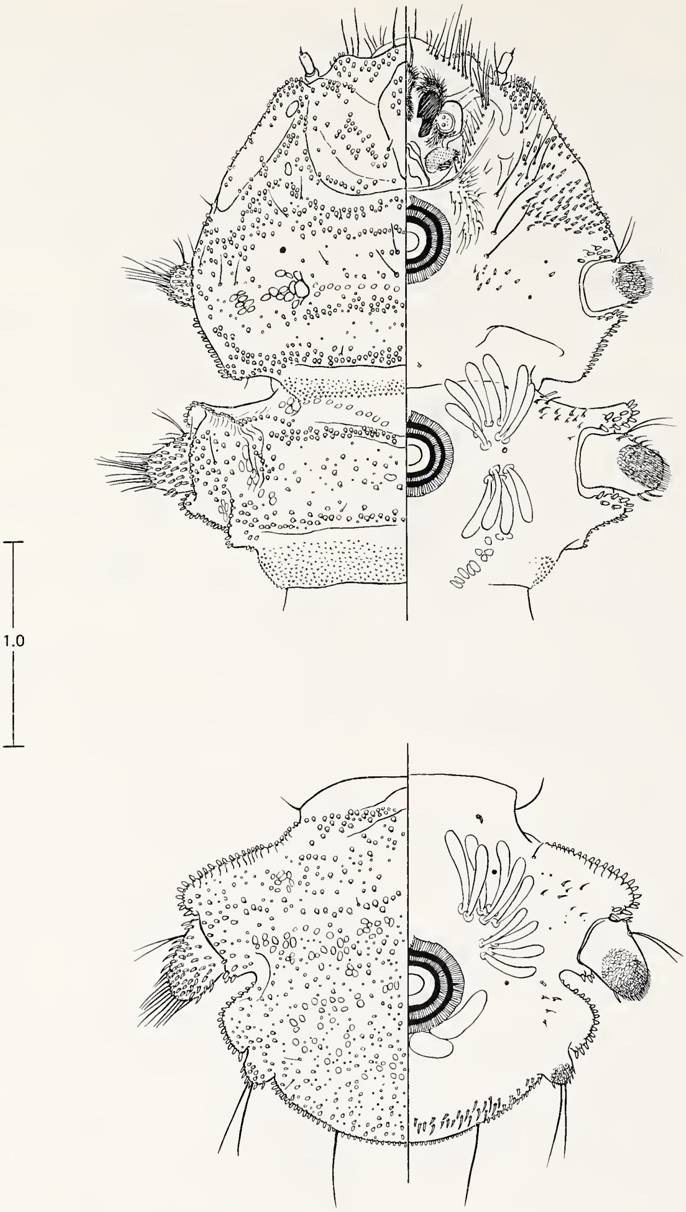


Figure 57. *Paltostoma saltana,* larva (dorsal view, left; ventral view, right).

on lateral convexity of abdominal segment VII. Sensilla of pseudopods setiform apically; dorsally modified, fustiform. Background field of small setiforms absent.

**SPECIMENS EXAMINED.** COLOMBIA, *Antioquia,* 1 km SE Paso de Boquerón, 22 Jun 1983, C.L. Hogue, CLH 300 (3 larvae).

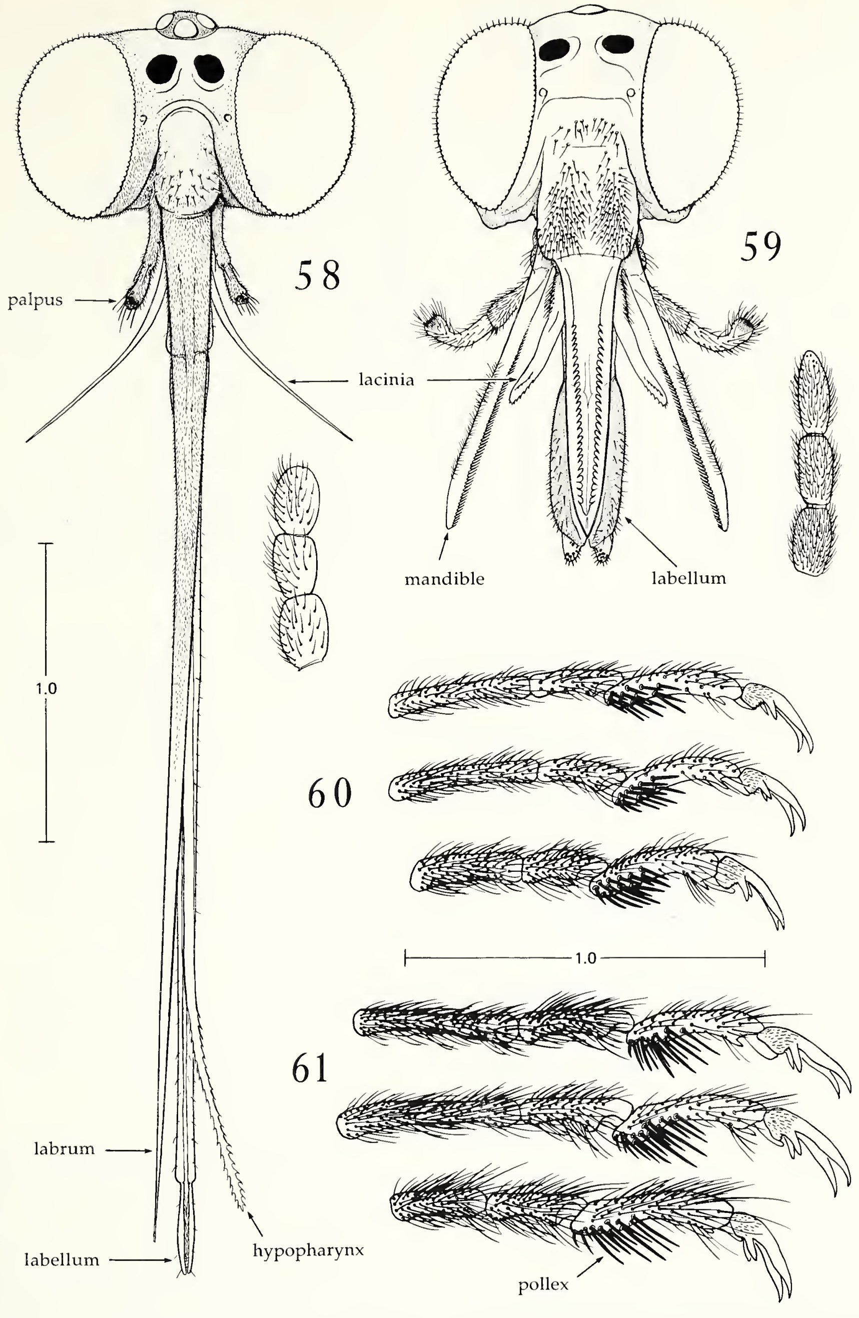
*Cundinamarca,* Río Frio, road from Zipaquira to Pacho, 2,900 m, 22 Jul 1967, P. & B. Wygodzinsky (12 larvae: AMNH).

**REMARKS.** Edwards' (1929) association of the male with the larva (which we assume to have been based only on sympatry), plus his inadequate description of the former, makes the identity of this species uncertain at this time. The larva that he figured in his original description (fig. 65) is unquestionably conspecific with ours from Antioquia and Cundinamarca but Edwards' figure of the female cotype is not diagnostic; likewise, his figure of an outer respiratory plate is insufficient to place the pupa.

## 6. *Paltostoma inca* Hogue, new species

Figures 49, 50, 58–65, 70, 74, 76

**DIAGNOSIS.** *Adult.*—Externally the adults of both sexes are somewhat similar to those of *P.*



**Figures 58–61.** *Paltostoma inca,* anatomical details labeled. **58.** Male head (frontal view) and terminal antennal segments (inset). **59.** Female head and terminal antennal segments (arrangements as for male). **60.** Terminal tarsal segments of male (fore leg, upper; mid leg, center; hind leg, lower; lateral view). **61.** Terminal tarsal segments of female (arrangement as for male).

*andeana,* but the male has a longer proboscis and the basal segment of the palpus is shorter in proportion to the distal (1.5) than in that species (2.0). Both male and female terminalia are very distinct (see Keys). *Pupa.*—The pupa keys out with those of *Limonicola medius* and *L. lichanos,* all with the abdominal tergites raised medially, but is distinguished most obviously from those species by the sparse papillae on the thorax (in these other two species the thorax is densely papillose). *Larva.*—The larva is very distinctive, being the only regional species with very large, spinelike, dorsolateral projections on the dorsa of abdominal segments I–VI.

**DESCRIPTION. Male** (Figs. 58, 60, 62–65). Only pharate specimens are available (dissected from pupae). *Coloration.* Indeterminable. *Size.* A medium-sized blepharicerid. Measurements (from pharate specimens on slides) (N = 2–3) (femur–tarsus 1 unextended and not measurable):

| | | fore leg |
|---|---|---|
| tarsus | 2 | 0.89 (0.89–0.89) |
| | 3 | 0.39 (0.37–0.42) |
| | 4 | 0.23 (0.22–0.25) |
| | 5 | 0.35 (0.32–0.37) |
| | | **mid leg** |
| tarsus | 2 | 0.87 (0.86–0.88) |
| | 3 | 0.41 (0.41–0.42) |
| | 4 | 0.23 (0.23–0.25) |
| | 5 | 0.36 (0.35–0.36) |
| | | **hind leg** |
| tarsus | 2 | 0.57 (0.56–0.59) |
| | 3 | 0.28 (0.28–0.29) |
| | 4 | 0.23 (0.22–0.24) |
| | 5 | 0.36 (0.35–0.37) |

*Head* (Fig. 58). Normal type, dichoptic. Eyes distant dorsally, interocular distance equal to 0.3 head width. Mouthparts well developed, proboscis extremely long, labium about 3.0 head width; palpus short, 2-segmented, basal segment elongate, 1.5 length of distal (=segment 3); sensory pit present. Antenna 15-segmented, flagellar segments elongate barrel-shaped, ultimate segment equal to penultimate, proportions of apical three segments 1.0–1.0–1.0.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals numerous, general; occipitals and postgenals indeterminable, apparently numerous, minute; labials and labellars numerous, scattered throughout.

*Thorax and appendages* (Fig. 60). Anal angle of wing produced, broadly lobular. Legs long and slender, hind legs stouter than others. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg n.a.–n.a.–n.a.–0.4–0.6–1.5; mid leg n.a.–n.a.–n.a.–0.5–0.6–1.6; hind leg n.a.–n.a.–n.a.–0.5–0.8–1.6; tarsomere 4 short in relation to 3 on fore and mid legs (0.6), hind leg longer (0.8). Tarsomeres 5 similar on all legs, curved, with extensive pollex of heavy setae; claw sickle-shaped, with sub-basal tooth and trichiate basally.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals and dorsocentrals apparently absent (specimens imperfect); prescutals indeterminable; supraalars several (6–7); prescutellars indeterminable; scutellars numerous, long and concentrated in a dense lateral group; preepisternals-episternals very numerous (33); metapleurals numerous (27–30); suprametapleurals few (4–5).

*Terminalia* (Figs. 62–65). Cerci parallel; interlobular depression deep, narrow, linear; individual cercus lobular, apex truncate. Tegmen very broad, apex furrowed, posterolateral margin with strong, arcuate fold extending mediad. Outer gonostylus moderately large, simple, obovate. Inner gonostylus an elongate, simple, porrect finger. Sperm sac small, boxlike, with anterolateral patches of spinulae on inner dorsal wall. Apodeme very small, horizontal, square. Aedeagal rods very long and slender. Lateral tine absent, no evidence of ventral plate. Gonite with very long corpus (compensating for extra wide tegmen). Xth segment conical.

Sensilla.—Epandrium with numerous medium setiforms in multiple, transverse series. Cercus with medium setiforms generally over apical half; setae of inner arm numerous and distributed along entire length nearly to apex of cercus. Outer gonostylus with medium setiforms general ectally; medium setiforms in basal and apical groups entally. Xth tergite with 4 alveoliforms sublaterally. Xth sternite with two long setiforms apically.

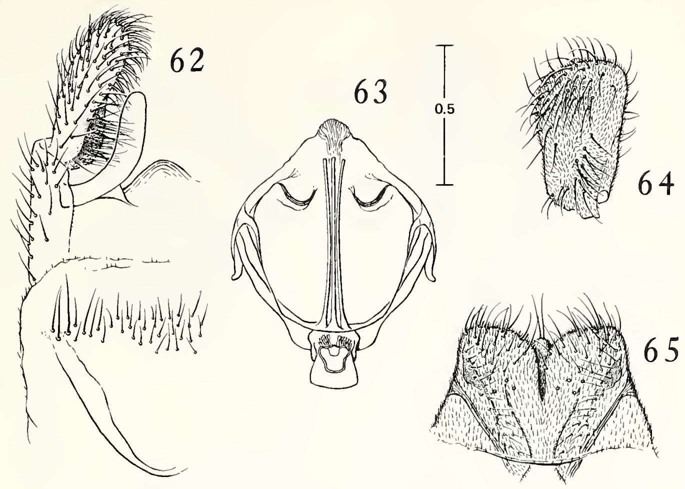
**Female** (Figs. 59, 61, 70). Only pharate specimens are available (dissected from pupae). *Coloration.* Indeterminable. Wing membane infuscate. *Size.* Apparently a medium-sized blephariceríd. Measurements (from pharate specimens on slides) (N = 2–3) (femur–tarsus 1 unextended and not measurable):

| | | fore leg |
|---|---|---|
| tarsus | 2 | 0.91 (0.86–0.97) |
| | 3 | 0.46 (0.46–0.47) |
| | 4 | 0.29 (0.25–0.32) |
| | 5 | 0.42 (0.41–0.44) |
| | | **mid leg** |
| tarsus | 2 | 0.86 (0.82–0.91) |
| | 3 | 0.46 (0.43–0.49) |
| | 4 | 0.31 (0.31–0.32) |
| | 5 | 0.41 (0.39–0.43) |
| | | **hind leg** |
| tarsus | 2 | 0.59 (0.54–0.62) |
| | 3 | 0.32 (0.31–0.34) |
| | 4 | 0.28 (0.27–0.30) |
| | 5 | 0.42 (0.40–0.44) |

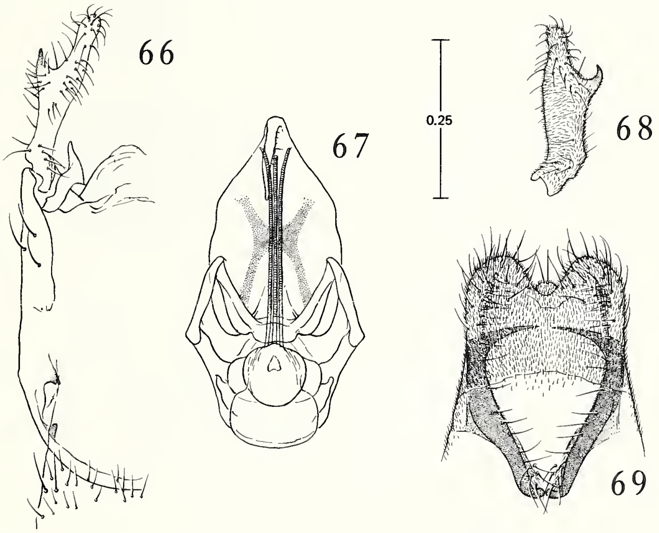
*Head* (Fig. 59). Normal type, dichoptic. Eyes disjunct dorsally, interocular distance 0.3 head width. Mouthparts well developed, mandibles and lacinia present and complete, former with filamentous projections along lateral margins; proboscis long, labium 1.1 head width; margin of hypopharynx strongly dentate. Palpus short, composed of very short basal segment and two elongate distal segments (=segments 2 and 3; proportions 1.0–1.2), sensory pit very well developed and terminal. Antenna 15-segmented, flagellar segments elongate cylindrical, ultimate slightly longer than penultimate, proportions of apical three segments 1.0–1.0–1.2.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals very numerous, general; posterior groups confluent, rear of head generally setate, including postgenal area; labials and labellars very numerous, general.

*Thorax and appendages* (Fig. 61). Anal angle of wing slightly convex, not lobular. Legs long and



**Figures 62–65.** *Paltostoma inca*, male terminalia (dorsal views). **62.** Genital capsule and gonostyli. **63.** Mesosomal structures and gonites. **64.** Left outer gonostylus (inner view). **65.** Cercal complex.

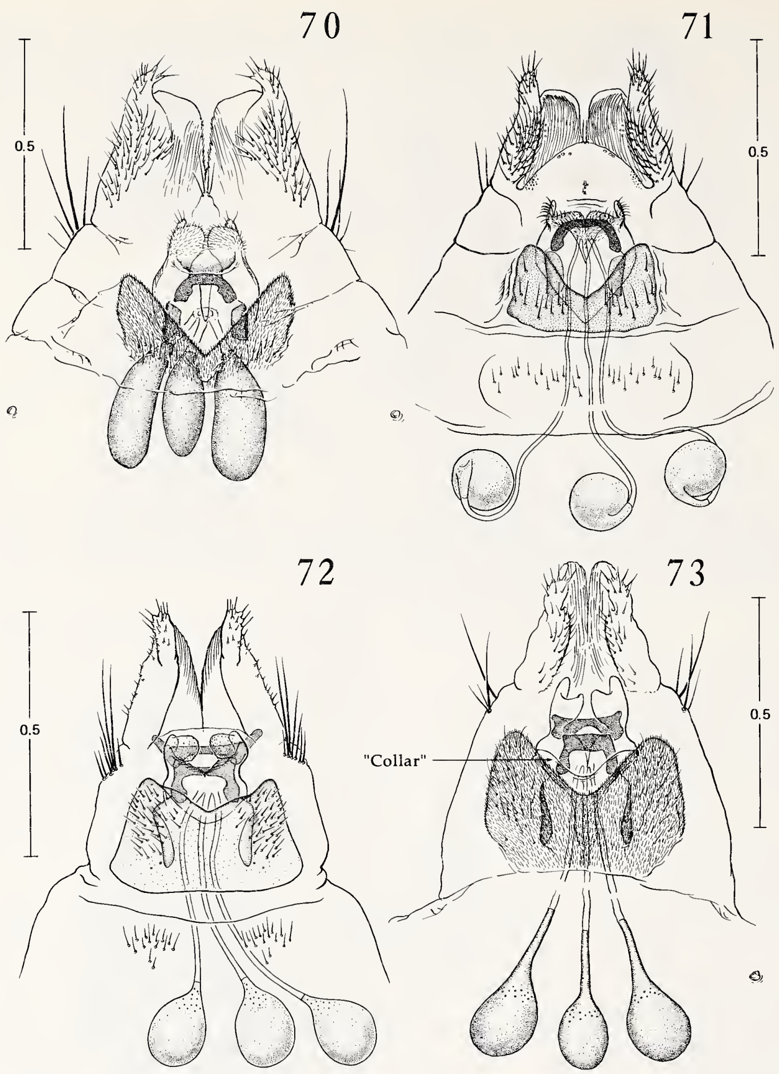


**Figures 66–69.** *Paltostoma andeana*, male terminalia (dorsal views). **66.** Genital capsule and gonostyli. **67.** Mesosomal structures and gonites. **68.** Left outer gonostylus (inner view). **69.** Cercal complex.

slender; hind legs somewhat stouter than other legs. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg n.a.–n.a.–n.a.–0.5–0.6–1.4; mid leg n.a.–n.a.–n.a.–0.5–0.7–1.3; hind leg n.a.–n.a.–n.a.–0.6–0.9–1.5; tarsomere 4 short in relation to 3 in fore and mid leg (0.6–0.7), long in hind leg (0.9). Tarsomeres 5 similar on all legs, with pollex of heavy setae, ventral group of slightly oversized setae present also subterminally; claw sickle-shaped, with sub-basal tooth and trichiate basally.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals scant; dorsocentral series undeveloped; prescutals numerous (11–16), a small subgroup of four to seven located ventrally just anterior to prescutal suture; supraalars few (1–3); prescutellars absent; scutellars numerous, and concentrated in a dense lateral group, numerous setae scattered mediad from group across posterior margin of sclerite; preepisternals and episternals numerous, former longer; metapleurals very numerous, a small ventral subgroup separated from main upper field; suprametapleurals few (3–4).

*Terminalia* (Fig. 70). Medial plate of the VIIIth sternite broad; lateral margin straight, medial depression deep, broadly V-shaped, medial internal sclerotization undeveloped; lobe somewhat narrow, straight, apex distant from hypogynial plate. Hypogynial plate complex, base slightly broader than lobes, lobe sessile (not on neck), dorsal division elongate, with few small setae, ventral division broad, generally with long microtrichiae. Spermathecae three, moderate-sized, medial smaller than



**Figures 70–73.** *Paltostoma* and *Limonicola,* female terminalia (ventral view). **70.** *P. inca.* **71.** *P. andeana.* **72.** *L. lichanos.* **73.** *L. astylis.*

laterals, all well sclerotized and similar in shape, elongate-oval, with short necks and short, straight ducts.

Sensilla.—Sternite VIII with seven to ten medium setiforms, distributed generally over lobe.

**Pupa** (Figs. 49, 50). *Integument.* Periphery abrupt, sclerotized integument underfolded and forming broad ventral border. Papillose dorsally. Papillae irregular in density and distribution. Individual papillae small, smooth, rounded, oval convexities. Papillar distribution as follows: scutum—sparse transverse group on disc; branchial sclerite—dense over most of surface to base of branchiae; metathoracic sclerite—dense throughout; abdominal tergites—generally dense, but slightly closer and smaller mediad than laterad.

*Size.* Medium for family. Measurements, male (N = 10): length 5.7 (5.5–5.9), width 3.7 (3.5–3.9); female (N = 10): length 6.3 (6.0–6.7), width 4.1 (3.9–4.7). Male 0.8 size of female.

*General.* Outline shape ovoid. Cross section depressed triangular. Dorsal sclerites: cephalic sclerite smooth. Branchial sclerite square, flat. Anterior margin of scutum smoothly and gently inclined. Abdominal tergites convex medially, forming a medially grooved, middorsal ridge; lateral margins entire.

*Branchiae.* Moderately large, erect; anterior and middle plates subparallel, all slightly divergent, posterior plates parallel, erect. Anterior and posterior plates rigid, heavily sclerotized, triangular, and about equal in size, with broad, membranous inner margins; inner two plates narrower, thinner and narrower than outers, entirely semimembranous.

**Larva** (Figs. 74–76). *General.* Body form lobiform. Medial elevated zones of abdominal seg-

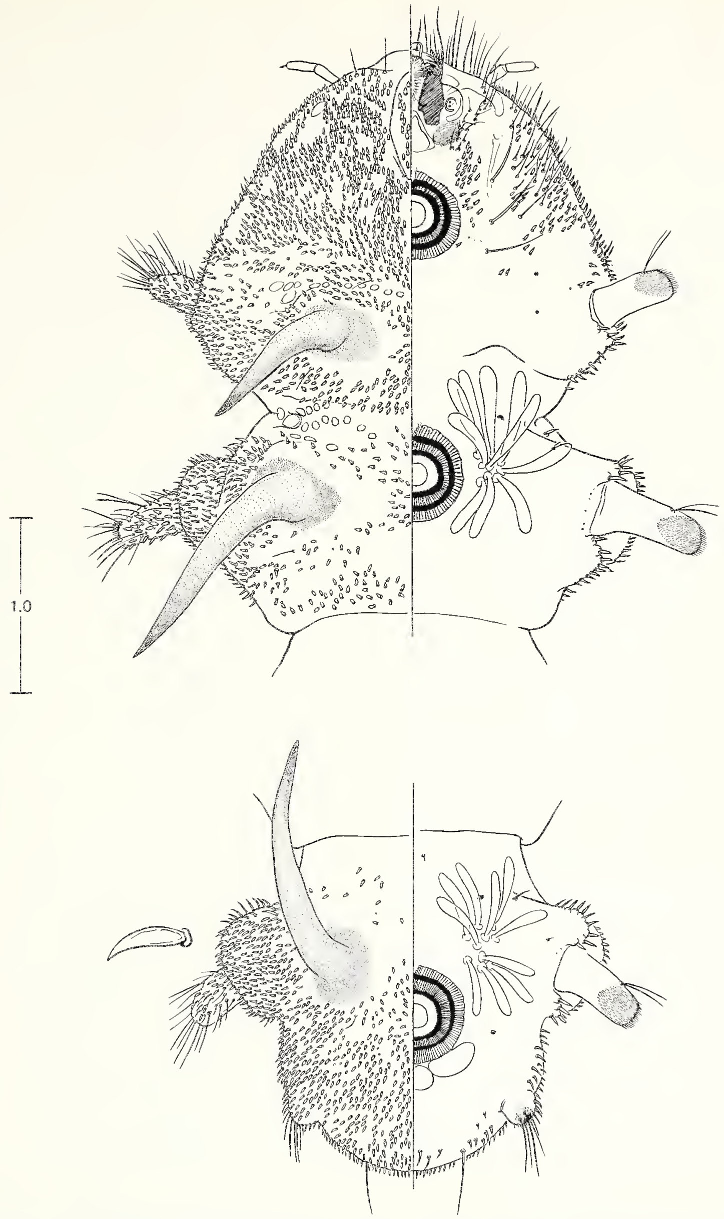


Figure 74. *Paltostoma inca,* larva (dorsal view, left; ventral view, right; typical modified sensillum, inset).

ments not developed. Outline shape of anterior division subovate.

*Integument.* Dorsum moderately well sclerotized. Corrugations distinct, fine, zig-zagging middorsally, becoming concentric and linear around bases of large, dorsal, spinelike projections. Venter with area at bases of pseudopods minutely strigulate.

*Coloration.* Trunk pigmentation even, sclerotized portions pale brown to black; terminal border unpigmented.

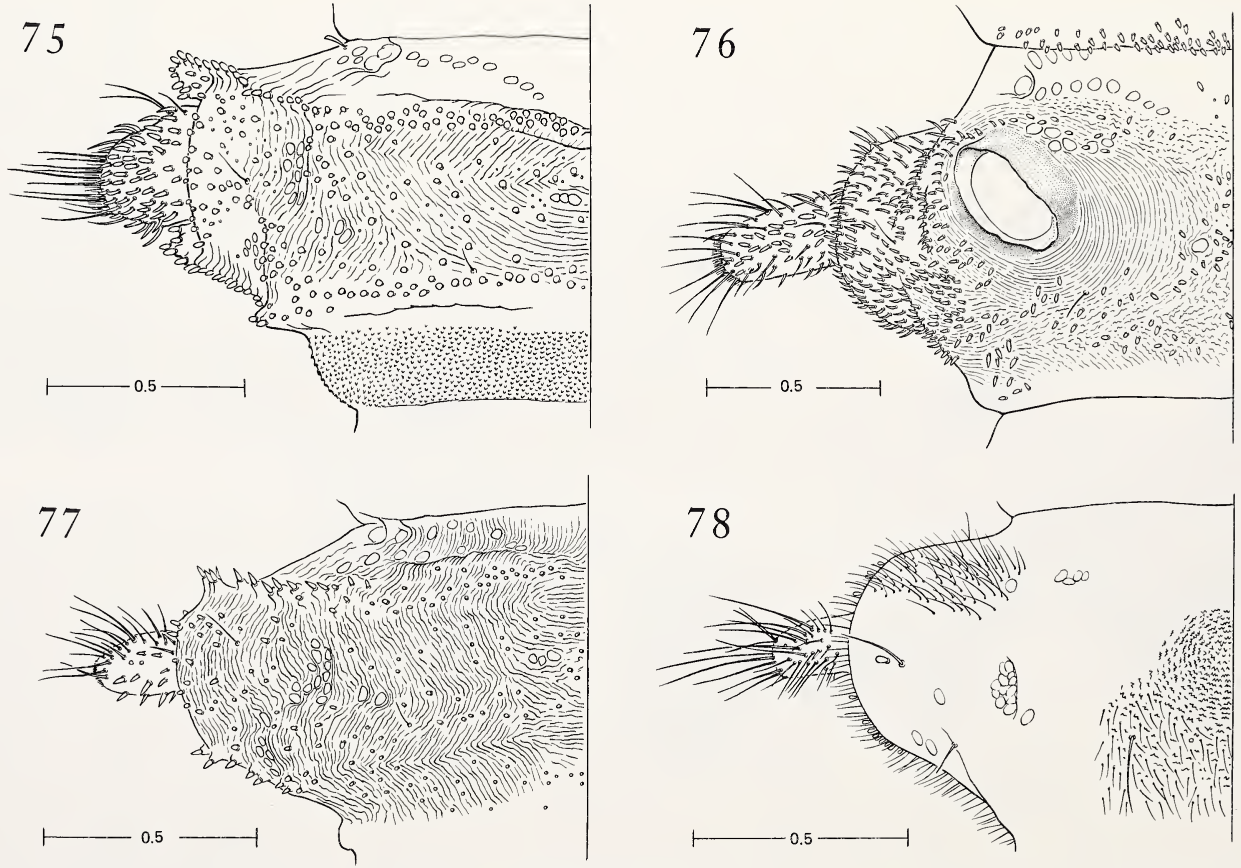
*Size.* medium for the genus. Measurements (N = 10): body length 9.2 (8.6–9.6), head capsule width 1.7 (1.4–1.8), antennal segment lengths, basal 0.11 (0.11–0.13), apical 0.14 (0.13–0.15).

*Head.* Antennal segment proportions 1.0–1.2.

*Trunk.* Dorsum of abdominal segments I–VI each with a pair of large, dorsolateral, sclerotized, smooth, erect, spinelike projections, with sharply acute apices; projection of abdominal segment I about one-half size of others.

*Anal division.* Dorsal pseudopod small, a nub, directed posterolaterad. Terminal incision not developed. Terminal lobe narrowed posteriad, with convex posterior margin.

*Primary sensilla* (medium setiforms unless oth-



Figures 75–78. *Paltostoma* and *Limonicola* larvae, abdominal segment III (left half, dorsal view). 75. *P. saltana.* 76. *P. inca.* 77. *P. andeana.* 78. *L. lichanos.*

erwise described). tM–T oblique, tM more medial. stM–T indiscernible; stI–VI posterior to base of spine; stVII and inner tpVII proximate. Inner tpP anteromedial to spiracle. Outer tpI–VI indiscernible. Terminal setae 1–1, widely separated.

*Dorsal modified sensilla.* Circumlateral series and ridges not developed. Small elongate oviform to pyriform types general on head sclerites and trunk segments, these more dense laterad than mediad; areas around bases of dorsal spinelike projections and projections themselves bare. Dorsal sensilla of pseudopods setiform apically and anteriorly, elongate ovoid to pyriform dorsally. Background field of fine setiforms absent.

**SPECIMENS EXAMINED.** Types: HOLOTYPE male (entirely dissected from pupa and mounted on slides nos. CLH 88-76H, 88-76B, 88-76W, and 88-76); ALLOTYPE female (entirely dissected from pupa and mounted on slides nos. CLH 88-79H, 88-79B, 88-79W, and 88-79); 2 male and 2 female PARATYPES (entirely dissected from pupae and mounted on slides): BOLIVIA, *La Paz,* small tributary to south of Río Unduari, 21.2 km W Puente Villa, 18 Jul 1988, C.L. Hogue, CLH 456 (LACM).

**Additional Specimens.** BOLIVIA, *La Paz,* same data as types (138 pupae, 56 larvae). Río Elena, 6.6 km E Yolosa, 17 Jul 1988, C.L. Hogue, CLH 453.1.1 (6 pupae, 7 larvae); 0.1 km E Puente Villa, 18 Jul 1988, C.L. Hogue, CLH 455 (28 pupae, 102 larvae); 15 km S Coripata, 18 Jul 1988, C.L. Hogue, CLH 454.1.1 (13 pupae, 53 larvae).

COLOMBIA, *Antioquia,* Quebrada La Espadera, 7.7 km E Medellín, 23 Jun 1983, C.L. Hogue, CLH 308 (2 larvae); 3 km N Palmitas, 22 Jun 1983, C.L. Hogue, CLH 301 (1 pupa).

*Valle,* Quebrada Honda, Peñas Blancas, 1,800 m, 3 Jun 1974, C.L. Hogue (36 larvae).

ECUADOR, *Pastaza,* 21 km W Puyo, 9 May 1977, P.J. Spangler, DRG-23 (2 pupae, 2 larvae).

*Pinchicha,* 58.2 km WNW Aloag, junction of highways 30 and 35 on road to Santo Domingo, 3,300 feet, 9 Jul 1973, J. Emmel (1 larva).

*Zamora-Chinchipe,* 14.4 km S Zumbi, 950 m, 4 Nov 1979, J. Anderson (1 larva).

PERU, *Junin,* San Ramón, Estancia Naranjal, 20–27 Jul 1965, P. & B. Wygodzinsky (8 pupae, 17 larvae: AMNH).

**ETYMOLOGY.** The species is named in honor of the historic Incan Empire, with whose geographic extent the insect's distribution generally coincides. The name is used in the nominative singular and in apposition to the generic appelation.

**REMARKS.** A series of larvae and a single pupa are all that have been taken in Antioquia Department. Until Hogue collected new material of all stages in 1988 in Bolivia, the association of larva and pupa could not be made. The specimens from Bolivia are the first of the family Blephariceridae that have been recorded in the literature from that country.

The larva is very different from any other from Antioquia Department in the possession of six pairs of very long, erect, dorsal spines. There are other species of *Paltostoma* and *Kelloggina* with similar-appearing processes; however, these are not strictly homologous organs, having slightly different places of origin from the dorsal body wall.

Association of the stages is certain (ontogenetic method).

### 7. *Paltostoma andeana*
### Hogue and Bedoya,
### new species

Figures 51, 52, 66–69, 71, 77, 79–83

*Paltostoma* sp. of Bedoya, 1984. Bedoya and Roldán, 1984:118, fig. 4d. Roldán, 1988: fig. 144. [All determinations based on larvae.]

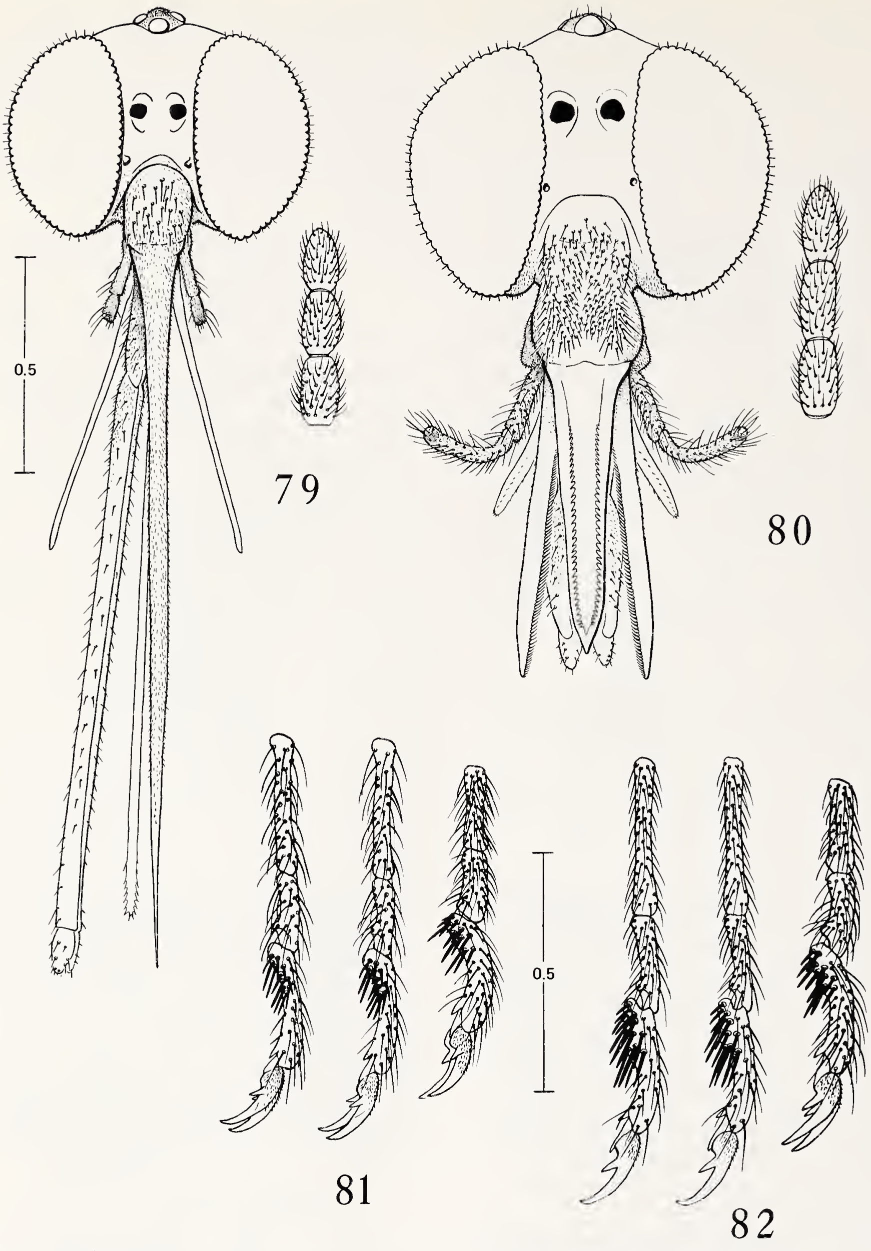
**DIAGNOSIS.** *Adult.*—The mouthparts of the male are like those of *inca,* with a 2-segmented palpus; the basal segment in the male is longer in proportion to the distal (2.0) than in that species (1.5). The female has well-developed mandibles also, unlike the other Antioquian *Paltostoma,* which lack these mouthpart structures. In the male terminalia the inner gonostylus is very short and with an acute apex rather than long and with a rounded apex as in *inca.* By the female terminalia the species can be immediately distinguished by its uniquely spherical spermathecae with adnate necks. *Pupa.*—This stage is unique among the blepharicerids of Antioquia by being hirsute (densely covered with bristlelike spines instead of papillae). *Larva.*—Only this among all the regional *Paltostoma* has an elongate basal antennal segment (0.7–1.0 distal); the larva is otherwise similar to that of *charadrae* and *eldorado.*

**DESCRIPTION.** Male (Figs. 66–69, 79, 81). Only pharate specimens are available (dissected from pupae). *Coloration.* Not available. *Size.* A medium-sized blephariceríd. Measurements (from one alcoholic and one pharate specimen on slide) (N = 1–2): wing length 5.0. Leg segment lengths [femur-tarsus 1 (except hind leg) unextended and not measurable]:

| | | fore leg |
|---|---|---|
| tarsus | 1 | |
| | 2 | 0.55 (0.54–0.57) |
| | 3 | 0.29 (0.29–0.29) |
| | 4 | 0.17 (0.16–0.18) |
| | 5 | 0.26 (0.26–0.26) |

| | | mid leg |
|---|---|---|
| tarsus | 1 | |
| | 2 | 0.59 (0.54–0.65) |
| | 3 | 0.30 (0.28–0.32) |
| | 4 | 0.17 (0.16–0.18) |
| | 5 | 0.24 (0.24–0.24) |

| | | hind leg |
|---|---|---|
| tarsus | 1 | 1.4 |
| | 2 | 0.34 (0.32–0.36) |
| | 3 | 0.18 (0.17–0.19) |
| | 4 | 0.16 (0.15–0.17) |
| | 5 | 0.25 (0.24–0.25) |



Figures 79–82. *Paltostoma andeana*. **79.** Male head (frontal view) and terminal antennal segments (inset). **80.** Female head and terminal antennal segments (arrangements as for male). **81.** Terminal tarsal segments of male (fore leg, left; mid leg, center; hind leg, right; lateral view). **82.** Terminal tarsal segments of female (arrangement as for male).

*Head* (Fig. 79). Normal type, subholoptic. Eyes disjunct dorsally, interocular distance equal to 0.2 head width; anterior eye margin entire. Mouthparts well developed, proboscis very long, labium 2.4–2.6 head width; palpus short, 2-segmented, basal segment elongate, 2.0 length of distal (=segment 3), sensory pit present. Antenna 15-segmented, flagellar segments barrel-shaped, ultimate segment slightly smaller (0.9) than penultimate, proportions of apical three segments 1.0–1.0–0.9.

Sensilla.—Setiforms on head capsule and mouthparts as follows: clypeals numerous, general; occipitals very numerous (30–35); postgenals few (4–5); labrals absent; labials and labellars numerous, scattered throughout.

*Thorax and appendages* (Fig. 81). Anal angle of wing produced, lobular. Legs long and slender, hind legs especially stout. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg n.a.–n.a.–n.a.–0.5–0.6–1.5; mid leg n.a.–n.a.–n.a.–0.5–0.6–1.4; hind leg n.a.–n.a.–0.3–0.5–0.9–1.5; tarsomere 4 short in relation to 3 on fore and mid leg (0.6), long on hind leg (0.9). Tarsomeres 5 similar on all legs, curved, with pollex of enlarged setae; claw sickle-shaped, with sub-basal tooth and trichiate basally.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; short dorsocentral series; prescutals several (8–11); supraalars few (3–4); prescutellars absent; scutellars numerous, long and concentrated in a dense lateral group, a few setae scattered mediad; preepisternals several (6–7); episternals numerous (15–16); metapleurals numerous (12–16), suprametapleurals few (3).

*Terminalia* (Figs. 66–69). Cerci parallel; interlobular depression shallowly U-shaped; individual cercus lobulate, with rounded apex. Subanal pouch with lateral walls modified into strongly sclerotized bars articulating with posterior lobe of gonite laterally and broadly fused with opposite member medially. Inner gonostylus short, triangular, apex acute. Inner walls of sperm sac with spinules. Ventral plate with a weak X-shaped sclerotization.

Sensilla.—Epandrium with numerous medium setiforms in transverse series. Cercus with medium setiforms mostly on apical third; setae of inner arm scattered along entire length, nearly to apex of cercus. Outer gonostylus with small setiforms general ectally; sparse basal and apical groups entally. Xth tergite with a pair of very short setiforms laterally. Xth sternite with two long setiforms apically.

**Female** (Figs. 71, 80, 82). Only pharate specimens are available (dissected from pupae). *Coloration.* Not available. *Size.* A medium-sized blephariccerid. Measurements (from pharate specimen on slide) (N = 1): wing length estimated at 5 mm. Leg segment lengths (femur–tarsus 1 unextended and not measurable):

| | | fore leg |
|---|---|---|
| tarsus | 2 | 0.62 |
| | 3 | 0.34 |
| | 4 | 0.21 |
| | 5 | 0.30 |

| | | mid leg |
|---|---|---|
| tarsus | 2 | 0.66 |
| | 3 | 0.34 |
| | 4 | 0.21 |
| | 5 | 0.28 |

| | | mid leg |
|---|---|---|
| tarsus | 2 | 0.38 |
| | 3 | 0.20 |
| | 4 | 0.17 |
| | 5 | 0.28 |

*Head* (Fig. 80). Normal type, dichoptic. Eyes disjunct dorsally, interocular distance 0.26 head width. Mouthparts well developed, mandibles and lacinia present and complete; proboscis long, labium 1.1 head width; margin of hypopharynx dentate; palpus short, composed of two elongate segments (=segments 2 and 3), proportions 1.0–1.4, sensory pit very well developed and terminal. Antenna 15-segmented, flagellar segments elongate barrel-shaped, ultimate subequal to penultimate, proportions of apical three segments 1.0–1.0–1.0.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals very numerous, general; occipitals very numerous; postgenals several (7); labrals absent; labials and labellars very numerous, general.

*Thorax and appendages* (Fig. 82). Anal angle of wing slightly convex, not lobular. Legs long and slender; hind legs somewhat stouter than other legs. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg n.a.–n.a.–n.a.–0.5–0.6–1.4; mid leg n.a.–n.a.–n.a.–0.5–0.6–1.3; hind leg n.a.–n.a.–n.a.–0.5–0.9–1.6; tarsomere 4 short in relation to 3 in fore and mid leg (0.6), long in hind leg (0.9). Tarsomeres 5 similar on all legs, with pollex of heavy setae, ventral group of slightly oversized setae present also subterminally; claw sickle-shaped, with sub-basal tooth and trichiate basally.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; dorsocentral series well developed; prescutals several to numerous (11–13); supraalars absent; prescutellars absent; scutellars numerous, long and concentrated in a dense lateral group, several setae scattered mediad from group; preepisternals several (8–9); episternals numerous (15–19); metapleurals several (12); suprametapleurals few (3).

*Terminalia* (Fig. 71). VIIIth sternite well sclerotized throughout, base broad; lateral margin straight, medial depression deep, broadly V-shaped, internal sclerotization keeled, irregularly quadrate; lobe straight, apex not closely appressed to hypogynial plate. Hypogynial plate complex, base as broad as lobes, lobes sessile, long microtrichiate, dorsal division elongate, ventral division broad. Spermathecae three, all similar, moderate-sized, well sclerotized, subspherical, necks short, strongly curved partially around corpus.

Sensilla.—Sternite VIII with 7–10 medium setiforms, distributed generally over lobe.

**Pupa** (Figs. 51, 52). *Integument.* Periphery abrupt, sclerotized integument underfolded and forming broad ventral border. Coarsely and densely set with long, slender, bristlelike spines in place of papillae. Individual spines very long and slender, with sharp apices and one or two very small basal spinelets (Fig. 52). Spine distribution as follows: scutum—moderately dense over entire disc, bristles shorter than elsewhere; branchial sclerite—dense over entire surface; metathoracic sclerite—along anterior half of sclerite only and shorter than elsewhere; abdominal tergites—dense over entire dorsum.

*Size.* Small for family. Measurements, male (N = 10): body length 3.1 (2.9–3.2), width 2.1 (2.0–2.2); female (N = 10): body length 4.1 (3.8–4.3), width 2.6 (2.4–2.8). Male 0.6 size of female.

*General.* Outline shape oval. Thorax somewhat narrowed in male but not abruptly. L/W male = 1.5, female 1.6. Dome-shaped in cross section; sides steeply inclined. Dorsal sclerites: cephalic sclerite smooth. Branchial sclerite taller than long, evenly rounded. Anterior margin of scutum smoothly and gently rounded. Suture separating metathoracic sclerite from abdominal tergite I smoothy rounded medially. Abdominal tergites smoothly convex middorsally (no medial ridges or nodes); lateral margins entire.

*Branchiae.* Moderately large, erect, anterior and middle plates parallel, posterior plates contiguous to overlapping apically. Individual plates rigid, triangular, with acute apices; inner third of outer plates lightly sclerotized (almost membranous); inner two plates slightly shorter, thinner, and narrower than outers; anterior plate somewhat broader than posterior.

**Larva** (Fig. 77, 83). *General.* Body form subonisciform. Medial elevated zones of abdominal segments well developed. Outline shape of anterior division broadly ovate.

*Integument.* Dorsum well sclerotized. Corrugations distinct, mostly linear, convergent across transverse anterior and posterior ridges. Venter with area at base of pseudopods strigulose, non-setate.

*Coloration.* Trunk brown, evenly pigmented; sclerotized portions dark brown, terminal border unpigmented.

*Size.* Medium for the family. Measurements (N = 10): body length 5.8 (5.6–6.1), head capsule width 1.3 (1.3–1.4), antennal segment lengths, basal 0.14 (0.13–0.15), apical 0.19 (0.17–0.23).

*Head.* Basal antennal segment elongate. Antennal segment proportions 1.0–1.3.

*Trunk.* Dorsum irregular, especially laterad: anterior transverse rounded convex ridge; lateral lobes anterior and posterior to bases of pseudopods of trunk segments, these stronger posteriad.

*Anal division.* Dorsal pseudopod a small nub, directed posterolaterad and projecting slightly beyond posterior margin. Terminal incision only slightly developed. Terminal lobe with convex, broadly rounded posterior margin.

*Primary sensilla* (medium setiforms unless otherwise described). tM–T oblique, tM more medial. Inner tpP anteromedial to spiracle. Outer tpI–VI indiscernible. Terminal setae 1–1, widely separated.

*Dorsal modified sensilla.* Pyriform to ellipsoid sensilla general on head sclerites. Moderate-sized pyriforms/oviforms in anterior and posterior transverse linear groupings on trunk segments, series linear on thorax, irregular on abdomen. Circumlateral series incomplete: extending only a short distance anteromedially; gap small so that anterolaterals and posterolaterals grouped on small convexities. Scattered small sensilla in area between rows and in posterior intersegmental zone. Sensilla of pseudopods setiform anteriorly and apically; dorsally and posteriorly acute to lanciform. Background field of small setiforms absent.

**SPECIMENS EXAMINED.** Types: HOLOTYPE male (dissected from pupa and partially mounted on slides nos. CLH 85-50 = terminalia and 86-630 = head); ALLOTYPE female (terminalia dissected from pupa and mounted on slide no. CLH 85-50); 13 male and 4 female PARATYPES (various terminalia and heads mounted on slides): COLOMBIA, *Antioquia,* Quebrada La Londoña, 9.3 km NW Palmitas, 12 Jun 1984, C.L. Hogue, CLH 321 (LACM).

**Additional Specimens.** COLOMBIA, *Antioquia,* same data as types (80 larvae, 128 pupae). Quebrada La Cristalina, 31 km W Doradal, 9 Jun 1986, C.L. Hogue, CLH 350.1 (1 larva, 2 pupae). Río Araña, 20 km S La Pintada, 17 Jun 1984, C.L. Hogue, CLH 333 (1 larva); 49.9 km E Marinilla, 14 Jun 1984, C.L. Hogue, CLH 326 (20 larvae, 3 pupae). Quebrada La Habana, 72.4 km E Marinilla, 14 Jun 1984, C.L. Hogue, CLH 328 (21 larvae); 78.1 km E Marinilla, 14 Jun 1984, C.L. Hogue, CLH 329.1 (59 larvae, 36 pupae); 13 km N Palmitas, 22 Jun 1983, C.L. Hogue, CLH 304 (109 larvae, 133 pupae); 7.4 km W Porce at km 54, 16 Jun 1985, C.L. Hogue, CLH 332 (1 larva, 1 pupa); 5.1 km E Río Calderas, Marinilla-Doradal, 14 Jun 1984, C.L. Hogue, CLH 327 (4 larvae). Quebrada La Hundida, 16.8 km E Santuario, 8 Jan 1986, C.L. Hogue, CLH 348.3.1 (3 larvae). Quebrada La Cascada, 65.9 km E Santuario, 10 Jan 1986, C.L. Hogue, CLH 351.1 (62 larvae, 30 pupae).

*Caldas,* Salto Lucio, 1 km SE Filadelfia, 17 Jun 1984, C.L. Hogue, CLH 335 (14 larvae); 6 km N Manizales, 17 Jun 1984, C.L. Hogue, CLH 336 (25 larvae, 36 pupae); 5 km N Supia, 17 Jun 1984, C.L. Hogue, CLH 334 (1 larva).

*Cundinamarca,* tributary to Río Sumapaz, km 86 Boquerón-Melgar Hwy, 8 Jun 1974, C.L. Hogue (19 larvae, 4 pupae).

*Tolima,* 3 km W Boquerón, 22 Jun 1984, C.L. Hogue, CLH 343 (1 larva, 1 pupa).

**ETYMOLOGY.** The name is an adjective, Latinized from the English "Andean" and arbitrarily assigned the neuter nominative ending "-a." It is used in reference to this species' occurrence in the Andes Mountains in contrast to the broader Caribbean or circum-Caribbean distribution of its relatives.

**REMARKS.** Association of the stages of *P. andeana* is certain, all by the ontogenetic method. This species is the most southern representative of a mainly Caribbean *Paltostoma schineri* group. All possess the "hirsute" type pupa and have several apomorphies well confirming the monophyly of the several species now known in the group: spermathecae of female terminalia with adnate necks, ventral margin of outer gonostylus of male terminalia with a conspicuous tooth midway. The larva, however, is unlike the typical Caribbean type, i.e., with segment VIII spatulate and with undeveloped dorsal pseudopods. It resembles the larvae of other species of *Paltostoma,* as for example, *P. eldorado.*

## LIMONICOLA Lutz

*Limonicola* Lutz, 1928:67. Type species: *Limonicola plurivectis* Lutz, 1928.

This is a fairly well-defined genus. Adults are characterized by their vestigial mouthparts and the large sperm sacs and absence of lateral tines in the male

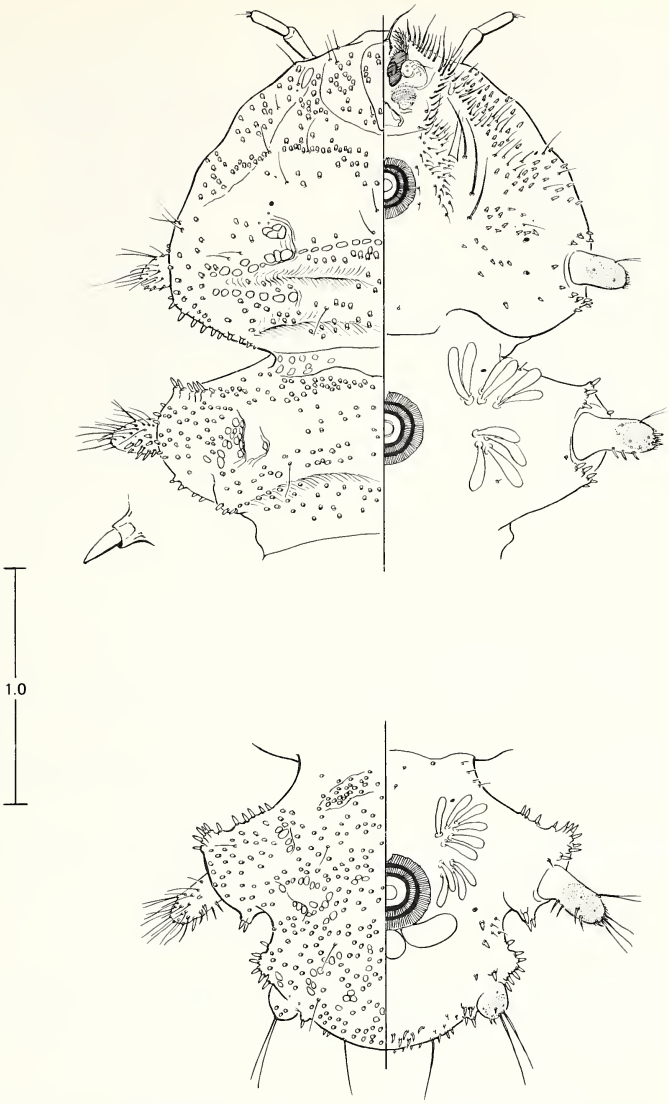


Figure 83. *Paltostoma andeana*, larva (dorsal view left, ventral view right; typical modified sensillum, inset).

terminalia. Also, the apex of the hind tibia and first two tarsal segments are inflated in the males of many species, a unique feature for blephariceridss. The branchial plates of the pupa are usually elongate, the posterior pair parallel to divergent; the larvae are lobiform, without clearly developed circumlateral series of modified sensilla. (See Keys for additional diagnostic features.)

Hogue's general collections contain many undescribed species of *Limonicola* from all parts of northwestern mainland South America; this may become the largest of all the neotropical genera. The genus apparently does not extend into Central America or southern South America.

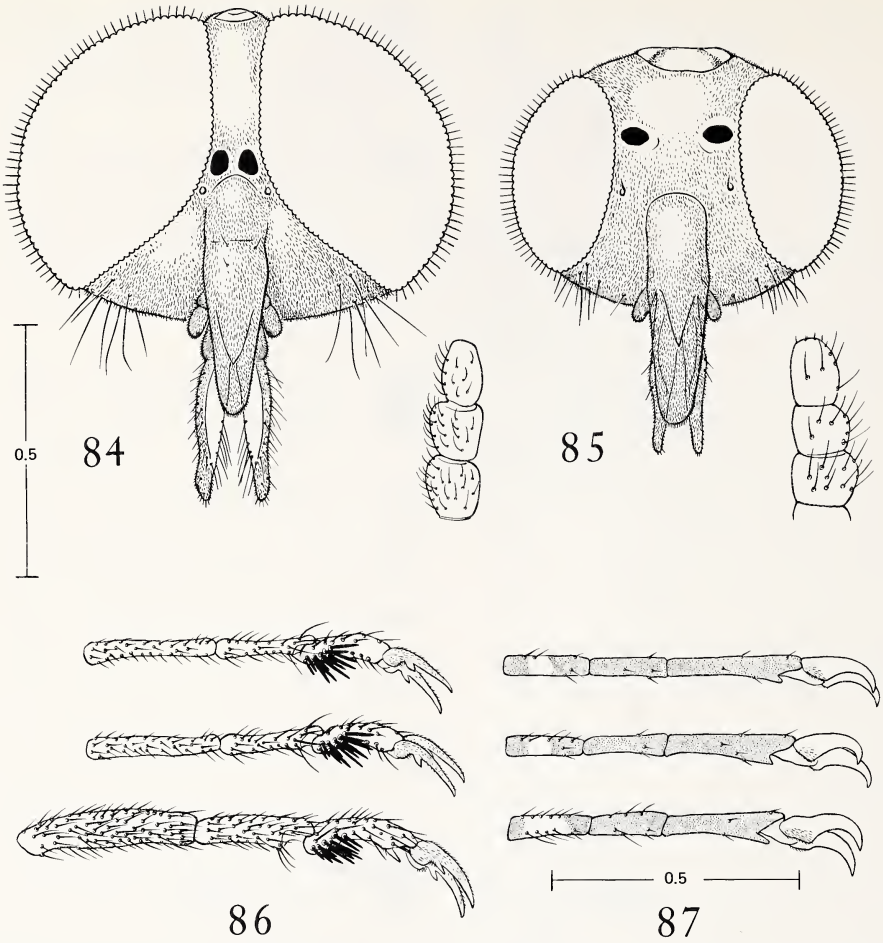
The name of the genus means "dweller in the Río Limón" (Spanish *Limon* = Río Limón, near Maracay, Venezuela, where the first species was discovered + Latin *cola* = dweller). The second part of the word is a common Latin noun that can be either masculine or feminine. The International Code of Zoological Nomenclature (1985) calls for such nouns to be treated as masculine [Art. 30a(i)]. Also, because the type species name is masculine, I believe that the generic name was intended to be of that gender.

## 8. *Limonicola lichanos* Hogue and Bedoya, new species

Figures 78, 84–91, 96–99, 101

*Limonicola* sp. 1 of Bedoya, 1984. Bedoya and Roldán, 1984:118, fig. 4b. Roldán, 1988: fig. 141. [All determinations based on larvae.]

**DIAGNOSIS.** *Adult.*—Male *lichanos* are the only regional *Limonicola* with equal flagellar segments in the antenna (including the ultimate) and normal,



**Figures 84–87.** *Limonicola lichanos.* **84.** Male head (frontal view) and terminal antennal segments (inset). **85.** Female head and terminal antennal segments (arrangements as for male). **86.** Terminal tarsal segments of male (fore leg, upper; mid leg, center; hind leg, lower; lateral view). **87.** Terminal tarsal segments of female (arrangement as for male).

non-inflated hind tarsi. The females have unusually short legs (combined femur–tibia only about half the length in other species). The elongate, straplike shape of the outer gonostylus in the male terminalia is unique. In the female terminalia the apex of the the VIIIth sternite lobe is characteristically produced and straight; in all other species, except *davila* in which it is incurved, the apex is unproduced. *Pupa.*—The pupa is very similar to that of *medius,* both densely papillose and otherwise identical; only the outline shape at the base of the outer margin of the anterior lamellar plate differs, in being excavate rather than entire (the bulla at the base is also less developed than it is in *medius*). *Larva.*—The larva is identified immediately by the bosses in the centers of abdominal segments I–VI.

**DESCRIPTION. Male** (Figs. 84, 86, 88–91). *Coloration.* Ground color velvety dark brown to black. Head, thorax, and abdomen with silvery pollinosity, forming irregularly appearing and disappearing patches as specimen is rotated in light from certain angles; legs dull brownish-black, without evident pollinosity. Wing membrane infuscate. *Size.* A medium-sized blepharicerid. Measurements (N = 7): wing length 3.7 (3.4–4.0). Leg segment lengths:

| | | fore leg |
|---|---|---|
| femur | | 1.2 (1.2–1.4) |
| tibia | | 1.5 (1.4–1.6) |
| tarsus | 1 | 1.2 (1.1–1.3) |
| | 2 | 0.49 (0.44–0.52) |
| | 3 | 0.31 (0.27–0.33) |
| | 4 | 0.18 (0.18–0.20) |
| | 5 | 0.21 (0.20–0.23) |

| | | mid leg |
|---|---|---|
| femur | | 1.4 (1.3–1.6) |
| tibia | | 1.5 (1.4–1.6) |
| tarsus | 1 | 1.1 (1.0–1.2) |
| | 2 | 0.46 (0.42–0.50) |
| | 3 | 0.29 (0.26–0.32) |
| | 4 | 0.18 (0.17–0.20) |
| | 5 | 0.21 (0.20–0.22) |

|  |  | hind leg |
|---|---|---|
| femur |  | 4.1 (3.6–4.3) |
| tibia |  | 3.9 (3.4–4.2) |
| tarsus | 1 | 1.5 (1.3–1.7) |
|  | 2 | 0.71 (0.65–0.76) |
|  | 3 | 0.50 (0.43–0.55) |
|  | 4 | 0.28 (0.21–0.31) |
|  | 5 | 0.24 (0.23–0.25) |

*Head* (Fig. 84). Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance 0.3 head width. Mouthparts poorly developed, proboscis very short, labium about 0.4 head width, labellar lobes parallel, lobe slightly sinuate, bladelike, constricted distad, palpus very short, a single diminutive segment, sensory pit absent, a single minute setiform on inner margin subapically. Antenna 15-segmented; flagellar segment 1 elongate, 1.6 length of segment 2, segments otherwise moniliform; ultimate segment slightly smaller (0.9) than penultimate, ovoid, proportions of apical three segments 1.0–1.0–0.9.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few (1–2); occipitals numerous (21–29); postgenals very numerous, long; labrals absent; labials absent; labellars numerous, scattered, long basally, few small setae apically.

*Thorax and appendages* (Fig. 86). Anal angle of wing produced, lobular. Legs moderately long, slender; fore femur sinuously curved, slightly incrassate; hind legs considerably longer but only slightly stouter than other legs. Tibial spurs 0–0–0. Progressive leg segment proportions: fore leg 1.2–0.8–0.4–0.6–0.6–1.2; mid leg 1.0–0.8–0.4–0.6–0.6–1.2; hind leg 1.0–0.4–0.5–0.7–0.6–0.9. Hind tarsal segments inflated; tarsomeres 5 similar on all legs, curved, with pollex of heavy setae; claw sickle-shaped, with sub-basal tooth and several trichiae between base and tooth.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichal and dorsocentral series absent; prescutals absent (a few–4 setae on anteromedial margin of scutum); supraalars few (2), far dorsal; prescutellars absent; scutellars numerous in lateral group; preepisternals several (7); metapleurals numerous (23); suprametapleurals few (5).

*Abdomen.* Pleural membranes of basal segments with long, sparse black hairs.

*Terminalia* (Figs. 88–91). Cerci divergent; interlobular depression very broadly V-shaped; individual cercus triangular, with rounded apex. Subanal pouch bowl-shaped, walls thin. Tegmen with truncate apex, latter slightly produced medially, with marginal sclerotization and with recurved medial dorsal keel; lateral margin strongly folded midway, fold extending mediad to midline. Outer gonostylus moderately large, an elongate, incurved, strap-shaped lobe. Inner gonostylus short, subtriangular, with produced, slightly angulate apex. Anterior lobes of gonites moderately expanded; apodeme small. Sperm sac large, with short longitudinal striae internally. Aedeagal rods moderately long and slender.

Sensilla.—Epandrium with numerous medium setiforms in transverse series. Cercus with medium setiforms mostly on apical third; setae of inner arm few and concentrated at anterior end. Outer gonostylus with medium setiforms general ectally; sparse basal and apical groups entally. Xth tergite with pair of very short setiforms sublaterally. Xth sternite with short setiform sublaterally.

**Female** (Figs. 85, 87). *Coloration.* As in male. Wing membrane infuscate. *Size.* A small blephariceridl. Measurements (N = 2): wing length 4.4 (4.4–4.4). Leg segment lengths (N = 3):

|  |  | fore leg |
|---|---|---|
| femur |  | 0.9 (0.8–1.0) |
| tibia |  | 0.9 (0.8–0.9) |
| tarsus | 1 | 0.5 (0.5–0.5) |
|  | 2 | 0.18 (0.16–0.20) |
|  | 3 | 0.15 (0.15–0.16) |
|  | 4 | 0.16 (0.16–0.17) |
|  | 5 | 0.28 (0.25–0.30) |

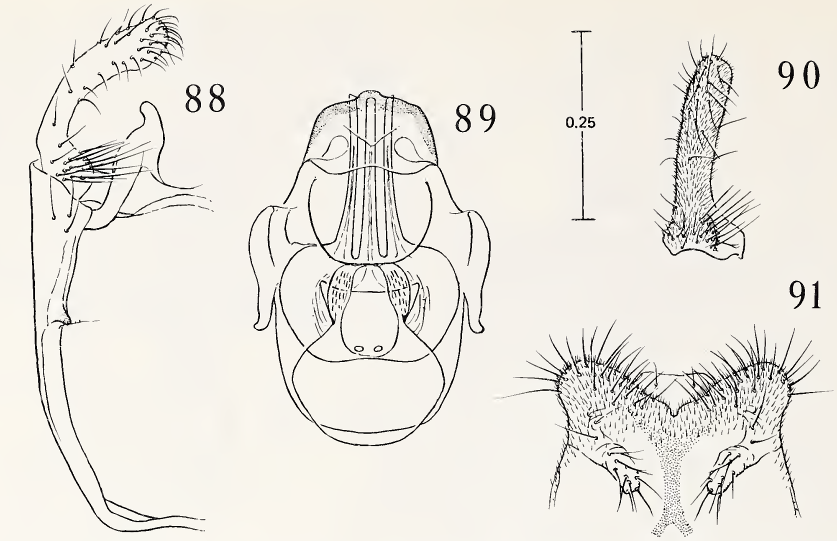
|  |  | mid leg |
|---|---|---|
| femur |  | 0.9 (0.8–1.0) |
| tibia |  | 0.8 (0.7–0.8) |
| tarsus | 1 | 0.4 (0.4–0.4) |
|  | 2 | 0.15 (0.15–0.15) |
|  | 3 | 0.14 (0.12–0.16) |
|  | 4 | 0.16 (0.15–0.17) |
|  | 5 | 0.28 (0.24–0.30) |

|  |  | hind leg |
|---|---|---|
| femur |  | 1.8 (1.7–2.0) |
| tibia |  | 1.6 (1.6–1.7) |
| tarsus | 1 | 0.4 (0.4–0.4) |
|  | 2 | 0.16 (0.16–0.17) |
|  | 3 | 0.15 (0.15–0.15) |
|  | 4 | 0.15 (0.15–0.16) |
|  | 5 | 0.27 (0.24–0.30) |

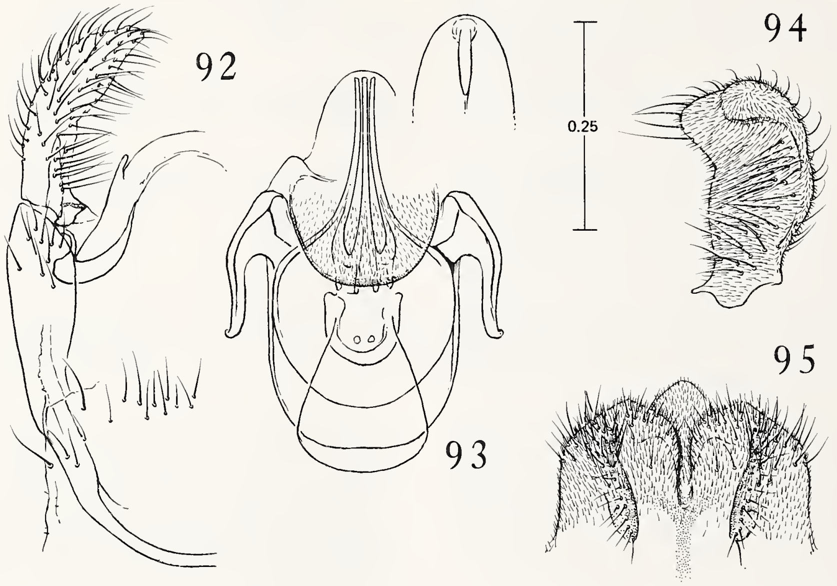
*Head* (Fig. 85). Similar to male. Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance 0.3 head width. Mouthparts poorly developed; mandibles and lacinia absent; proboscis very short, labium about 0.4 head width, labellar lobes divergent, lobe broad basally, slightly constricted distally; palpus very short, a single diminutive segment (=segment 3), sensory pit absent. Antenna 15-segmented, flagellar segments moniliform, ultimate segment slightly smaller (0.9) than penultimate, proportions of apical three segments 1.0–1.0–0.9.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few (2); occipitals numerous (15–18); postgenals very numerous and long; labrals and labials absent; labellars in two groups: numerous (11–13), longer basally, few (3–4), minute apically.

*Thorax and appendages* (Fig. 87). Anal lobe of wing produced, lobular. Legs short. Fore femur sinuously curved, strongly incrassate. Tibial spurs 0–0–0. Progressive leg segment proportions: fore leg 1.0–0.6–0.4–0.9–1.1–1.7; mid leg 0.9–0.5–0.4–0.9–1.1–1.8; hind leg 0.9–0.2–0.4–0.9–1.1–1.8; tar-



**Figures 88–91.** *Limonicola lichanos,* male terminalia (dorsal views). **88.** Genital capsule and gonostyli. **89.** Mesosomal structures and gonites. **90.** Left outer gonostylus (inner view). **91.** Cercal complex.

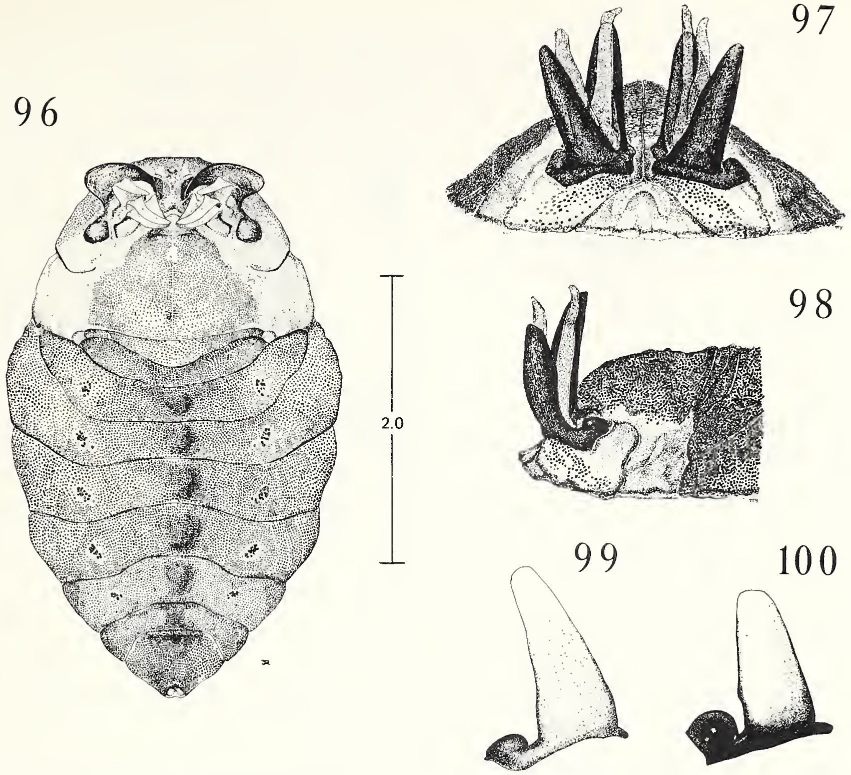


**Figures 92–95.** *Limonicola astylis,* male terminalia (dorsal views). **92.** Genital capsule and gonostyli. **93.** Mesosomal structures and gonites. **94.** Left outer gonostylus (inner view). **95.** Cercal complex.

somere 4 of all legs slightly longer than 3 (1.2), tarsomeres 5 all similar, straight, slightly expanded apically; claws simple, hook-shaped.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; dorsocentral series complete; prescutals absent; supraalars several (5), far dorsal; prescutellars several; scutellars very numerous, long and concentrated in group laterally, none scattered mediad; preepisternals several (8), long; episternals absent; metapleurals numerous (15–17); suprametapleurals few (4–5).

*Terminalia* (Fig. 72). VIIIth sternite well sclerotized throughout, base broad and well defined, with small sclerotization at basal corners; lateral margin straight, medial depression shallow, very broadly V-shaped, internal sclerotization flat, fusiform; lobe straight, lobes originating from base of sclerite, apex not closely appressed to hypogynial plate. Hypogynial plate complex, base as broad as lobes, lobe with broad neck, dorsal division short, lobulate, ventral division broad, weakly denticulate laterally, denticulae becoming better defined mediad. Spermathecae three, moderate-sized, well sclerotized, and with minute clear pits on proximal third, all similar, pear-shaped, with smooth outline, necks short and straight.



**Figures 96–100.** *Limonicola,* pupae. **96.** *L. lichanos,* entire, dorsal view. **97.** Same, frontal view. **98.** Same, anterior portion, lateral view. **99.** Same, anterior branchial plate (anterior view). **100.** *L. medius,* anterior branchial plate (anterior view).

Sensilla.—Sternite VIII with 30–35 medium setiforms, distributed generally over lobe.

**Pupa** (Figs. 96–99). *Integument.* Periphery abrupt, sclerotized ventral border present. Papillose dorsally. Papillae even and very dense (individual papillae nearly contiguous). Individual papillae subequal, small, smooth, rounded, oval convexities. Papillar distribution as follows: scutum—dense over entire disc; branchial sclerite—dense over entire surface; metathoracic sclerite—even and dense over entire surface; abdominal tergites—even and dense except for medial bosses where they are denser.

*Size.* Small for family. Measurements, male (N = 10): body length 3.8 (3.6–4.1), width 2.3 (2.0–2.5); female (N = 10): body length 3.9 (3.7–4.3), width 2.4 (2.1–2.7). Male 0.9 size of female.

*General.* Outline shape ovoid, thorax abruptly narrowed, more so in male than female. L/W male = 1.7, female 1.6. Cross section obtusely subtriangular; upper sides moderately inclined. Dorsal sclerites: cephalic sclerite irregular, with slight paramedial convexities. Branchial sclerite longer than tall, smoothly rounded and not projecting beyond cephalic sclerite. Anterior margin of scutum moderately inclined, not lobed. Suture separating metathoracic sclerite from abdominal tergite I V-shaped medially. Abdominal tergites with slight, anteromedial bosses; lateral margins entire.

*Branchiae.* Large, erect, anterior plates divergent, middle and posterior plates parallel. Outer plates subtriangular, elongate, broadly rounded apically; inner plates strap-shaped, much narrower than outer and slightly longer (exserted); outer margin of anterior plate entire; anterior plate expanded posterobasally to form a moderate-sized, slightly flattened bulla.

**Larva** (Figs. 78, 101). *General.* Body form generally lobiform. Outline shape of anterior division angular, subhexagonal.

*Integument.* Dorsum moderately well sclerotized. Corrugations distinct, fine, irregular throughout, except denser and arranged in a circular pattern around central node of abdominal segments I–VI. Venter with extensive (extending anterior and posterior to base of pseudopod), oval patches of strong denticulae medial to bases of pseudopods.

*Coloration.* Trunk light brown, evenly pigmented; sclerotized portions pale brown, except terminal border black.

*Size.* Medium for the genus. Measurements (N = 10): body length 5.1 (4.7–5.4), head capsule width 1.0 (1.0–1.0), antennal segment lengths, basal 0.04 (0.04–0.05), apical 0.15 (0.14–0.16).

*Head.* Antennal segment proportions 1.0–3.4.

*Trunk.* Dorsum of abdominal segments I–VI with a central boss or low, rounded convexity.

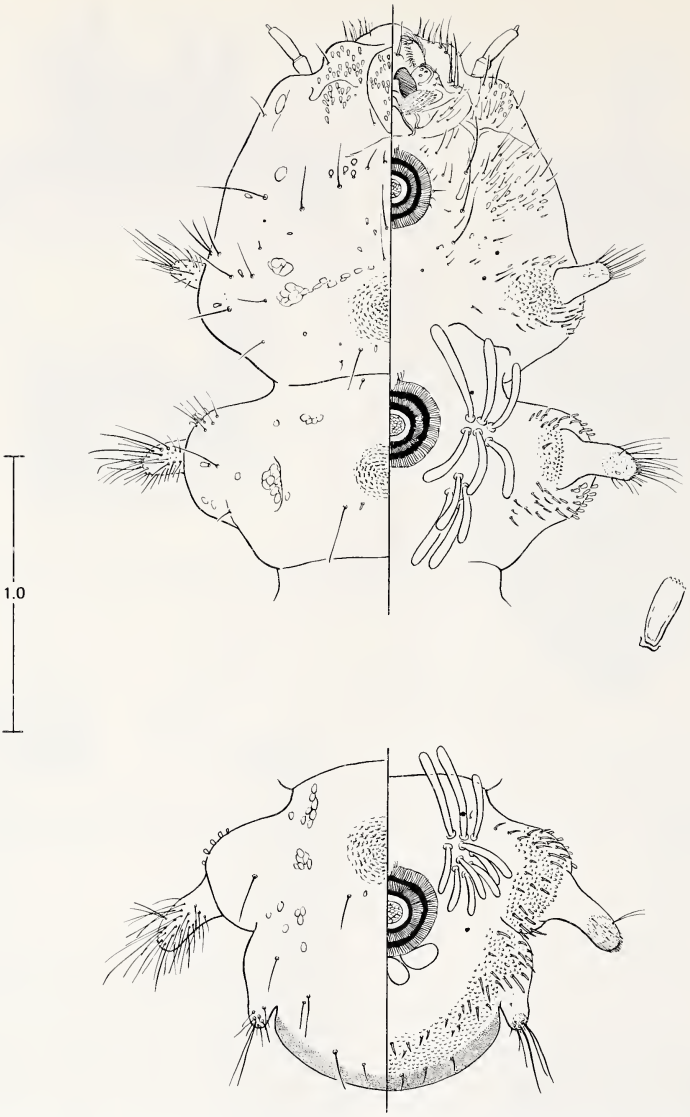


**Figure 101.** *Limonicola lichanos,* larva (dorsal view, left; ventral view, right; typical modified sensillum, inset).

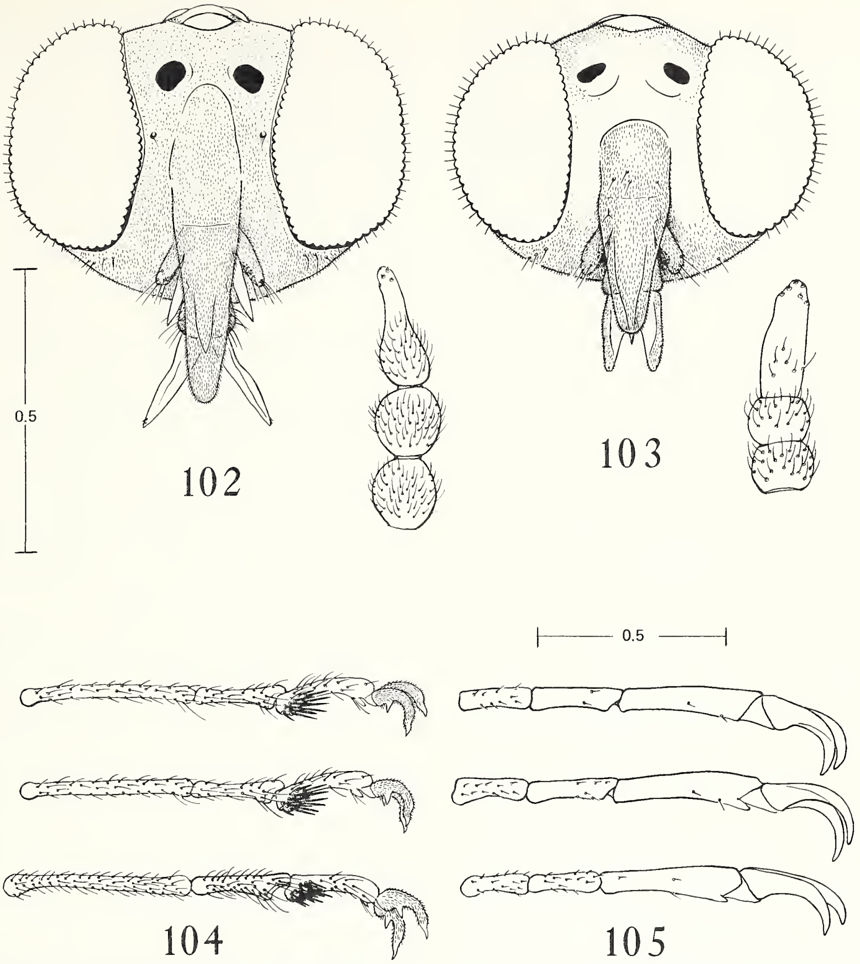
*Anal division.* Dorsal pseudopod small, lobular, directed posteriad. Terminal incision narrowly V-shaped. Terminal lobe broad, with arcuate posterior margin.

*Primary sensilla* (medium setiforms unless otherwise described). tM–T in line, long; tI–VI minute, pyriform. stM–T indiscernible; stVII and inner tp proximate. Inner tpP long, anteromedial to spiracle. Outer tpI–VI apparently lateral to inner tp, small, pyriform. Terminal setae 3–3, very short, chaetiform, submarginal, inserted ventrally.

*Dorsal modified sensilla.* Small obovate types in linear series and patches on head sclerites. Trunk segments with only a few, small pyriforms and setiforms laterally around base of pseudopod. Dorsal sensilla of pseudopods all setiform. Integument set with general background field of small, fine setiforms (except on central boss).

**SPECIMENS EXAMINED.** Types: HOLOTYPE male (terminalia mounted on slide no. CLH 87-168; 9 male PARATYPES (1 with terminalia mounted on slide no. 87-167): COLOMBIA, *Antioquia,* Quebrada La Hundida, 16.8 km E Santuario, 8 Jan 1986, C.L. Hogue, CLH 348.1 (LACM).

**Additional Specimens.** COLOMBIA, *Antioquia,* no specific locality, Aug 1983, I. Bedoya, 1 (5 larvae); Aug 1983, I. Bedoya, 3 (1 larva); Aug 1983, I. Bedoya, 7 (6 larvae). Quebrada Salado, 14 Jun 1984, C.L. Hogue, CLH 325 (2 females, 1 larva, 1 pupa). Quebrada Santo Domingo, 16 Jun 1984, C.L. Hogue, CLH 330 (8 males); 7.6 km S Porce, 16 Jun 1984, C.L. Hogue, CLH 332 (1 male, 2 larvae, 2 pupae); 7.6 km W Porce at km 57, 16 Jun 1984, C.L. Hogue, CLH 332 (3 males, 2 pupae, 3 larvae). Río Medellín, Primavera, 24 Jun 1983, C.L. Hogue, CLH 313 (580 larvae, 356 pupae).



**Figures 102–105.** *Limonicola astylis.* **102.** Male head (frontal view) and terminal antennal segments (inset). **103.** Female head and terminal antennal segments (arrangements as for male). **104.** Terminal tarsal segments of male (fore leg, upper; mid leg, center; hind leg, lower; lateral view). **105.** Terminal tarsal segments of female (arrangement as for male).

*Caldas,* 5 km N Supia, 17 Jun 1984, C.L. Hogue, CLH 334 (2 larvae).

*Cundinamarca,* Río Caqueza, 9 km NW Caqueza, 14 Apr 1981, C.L. Hogue, CLH 277 (2 males, 38 larvae, 15 pupae). Tributary to Río Caqueza, 1 km NE exit of Carrera 78 to Une, 15 Apr 1981, C.L. Hogue, CLH 279 (6 pupae).

*Quindio,* Río Quindio, 10 km N Armenia, Boquia, 18 Jun 1984, C.L. Hogue, CLH 337 (16 larvae, 123 pupae). Quebrada Salado, 4 km E Calarcá, 20 Jun 1984, C.L. Hogue, CLH 338 (1 male).

*Valle,* km 23 Cali-Dagua Highway (72A), 2 Jun 1974, C.L. Hogue (15 larvae, 1 pupa).

**ETYMOLOGY.** The name is a masculine noun in the nominative case transliterated from Greek and used in apposition to the generic name; it refers to the digitiform shape of the outer lobe of the dististyle (Greek *lichanos* = fore finger).

**REMARKS.** The imagos of this and *L. astylis* are very similar, certainly indicating close relationship. The similarity extends to *L. davila* and *medius,* the four species forming a complex with fairly similar immatures. The larvae of *astylis* and *medius* are not known but could be similar to larvae of either of the two other species (see Remarks under *L. medius* and *astylis*).

We have abundant material and are able to associate all the stages of this species with certainty using the ontogenetic criterion.

We have one male which differs slightly from the typical *L. lichanos,* the tip of the inner gonostylus being angled outward instead of straight. It may represent a closely related species, but we are considering it as a variant of *L. lichanos* for the present.

## 9. *Limonicola astylis* Hogue, new species

Figures 73, 92–95, 102–105

**DIAGNOSIS.** *Adult.*—The elongate, flask-shaped terminal antennal segment is distinctive for both sexes of *astylis,* as are the very small inner gonostylus (mostly fused with the aedeagal guide) and complex lobular shape of the outer gonostylus in the male terminalia. *Pupa and larva.*—Unknown.

**DESCRIPTION. Male** (Figs. 92–95, 102, 104). *Coloration.* Ground color deep, velvety blackish red-brown. Entire body, except antenna and legs, with silvery pollinosity, forming irregularly appearing and disappearing patches as specimen is rotated in light from certain angles; antenna and legs dull, without evident pollinosity. Wing membrane infuscate. *Size.* A medium-sized blepharicerid. Male considerably smaller than female. Measurements (N = 10): wing length 4.2 (3.9–4.5). Leg segment lengths:

| | | fore leg |
|---|---|---|
| femur | | 1.7 (1.5–1.8) |
| tibia | | 1.9 (1.7–2.1) |
| tarsus | 1 | 1.3 (1.1–1.4) |
| | 2 | 0.70 (0.58–0.89) |
| | 3 | 0.45 (0.42–0.49) |
| | 4 | 0.23 (0.21–0.26) |
| | 5 | 0.23 (0.21–0.25) |

| | | mid leg |
|---|---|---|
| femur | | 2.1 (1.9–2.4) |
| tibia | | 2.1 (1.8–2.8) |
| tarsus | 1 | 1.2 (1.0–2.0) |
| | 2 | 0.64 (0.60–0.74) |
| | 3 | 0.45 (0.41–0.50) |
| | 4 | 0.23 (0.21–0.25) |
| | 5 | 0.23 (0.21–0.26) |

| | | mid leg |
|---|---|---|
| femur | | 3.6 (3.3–4.0) |
| tibia | | 3.5 (3.3–4.0) |
| tarsus | 1 | 1.4 (1.3–1.5) |
| | 2 | 0.71 (0.65–0.83) |
| | 3 | 0.49 (0.45–0.53) |
| | 4 | 0.23 (0.22–0.28) |
| | 5 | 0.24 (0.22–0.27) |

*Head* (Fig. 102). Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance 0.3 head width. Mouthparts poorly developed, proboscis very short, labium about 0.4 head width, labellar lobes divergent, lobe bladelike, with sharply acute apices; palpus very short, a single diminutive segment, sensory pit absent. Antenna 15-segmented, flagellar segments moniliform, ultimate segment elongate, flask-shaped, longer (1.9) than penultimate, proportions of apical three segments 1.0–1.0–1.9.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few (2–3); occipitals several (6–7); postgenals few (4–5); labrals and labials absent; labellars few, scattered, minute.

*Thorax and appendages* (Fig. 104). Anal angle of wing produced, lobular. Legs long and slender; fore femur sinuously curved, incrassate; hind legs stouter and considerably longer than other legs. Tibial spurs 0–0–0. Progressive leg segment proportions: fore leg 1.1–0.7–0.6–0.7–0.5–1.0; mid leg 1.0–0.6–0.5–0.7–0.5–1.0; hind leg 1.0–0.4–0.6–0.6–0.5–1.0; tarsomere 4 short in relation to 3 in all legs (0.5). Hind tibia and tarsus slender throughout, no segments or portions inflated; tarsomeres 5 similar on all legs, curved, with pollex of heavy setae; claw sickle-shaped, with sub-basal tooth and trichiate basally, apex acuminate, curved.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals and dorsocentral series complete; prescutals several (11); supraalars absent; prescutellars several (11); scutellars very numerous, long and concentrated in group laterally, none medially; preepisternals several (5–6); metapleurals numerous (17); suprametapleurals few (4).

*Terminalia* (Figs. 92–95). Cerci parallel; interlobular depression fairly deep but narrow; individual cercus elongate with pointed apex. Subanal pouch with thin walls, inner surface covered with microtrichia. Outer gonostylus moderately large, an irregular, rectangular lobe with a slight inner, apicoventral boss, and produced slightly apicodorsally. Inner gonostylus mostly fused with aedeagal guide, apex represented by small tooth on lateral margin of guide. Anterior lobes of gonites moderately expanded; apodeme small. Sperm sac large. Aedeagal rods moderately long.

Sensilla.—Epandrirum with numerous medium setiforms in transverse series. Cercus with medium setiforms generally over apical half; setae of inner arm few but distributed along entire length. Outer gonostylus with medium setiforms general ectally; a dense elongate patch of moderately large setiforms along ental surface ventrally. Xth tergite with pair of very short setiforms sublaterally. Xth sternite with short setiform sublaterally.

**Female** (Figs. 73, 103, 105). *Coloration.* As in male. Wing membrane infuscate. *Size.* A medium-sized blepharicerid. Male considerably smaller than female. Measurements (N = 2): wing length 6.1 (5.3–6.9). Leg segment lengths:

| | | fore leg |
|---|---|---|
| femur | | 1.4 (1.3–1.6) |
| tibia | | 1.4 (1.2–1.7) |
| tarsus | 1 | 0.8 (0.7–0.9) |
| | 2 | 0.25 (0.19–0.30) |
| | 3 | 0.17 (0.14–0.20) |
| | 4 | 0.21 (0.20–0.23) |
| | 5 | 0.35 (0.33–0.37) |

| | | mid leg |
|---|---|---|
| femur | | 2.0 (1.8–2.2) |
| tibia | | 1.5 (1.4–1.7) |
| tarsus | 1 | 0.7 (0.6–0.7) |
| | 2 | 0.24 (0.20–0.28) |
| | 3 | 0.16 (0.12–0.19) |
| | 4 | 0.22 (0.20–0.23) |
| | 5 | 0.34 (0.31–0.37) |

| | | mid leg |
|---|---|---|
| femur | | 3.2 (2.9–3.6) |
| tibia | | 2.6 (2.3–2.8) |
| tarsus | 1 | 0.6 (0.6–0.6) |
| | 2 | 0.22 (0.18–0.26) |
| | 3 | 0.15 (0.12–0.17) |
| | 4 | 0.19 (0.17–0.20) |
| | 5 | 0.32 (0.30–0.34) |

*Head* (Fig. 103). Described from a single specimen. Similar to male. Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance 0.3 head width. Mouthparts poorly developed; mandibles and lacinia absent; proboscis very short, labium about 0.4 head width, labellar lobes divergent, lobe bladelike; palpus very short, a single diminutive segment (=segment 3), sensory pit absent, replaced by several alveoliform sensilla in group on inner surface. Antenna 15-segmented, flagellar segments moniliform, ultimate segment elongate, longer (2.8) than penultimate, proportions of apical three segments 1.0–1.0–2.8.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few (3); occipitals several (8–10); postgenals few (2–5) small; labrals absent; labials few, scattered; labellars few (2) basally, few (1–2) apically.

*Thorax and appendages* (Fig. 105). Described from two specimens (one with missing head). Anal angle of wing produced, lobular. Legs long and slender. Fore femur sinuously curved, incrassate. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg 1.0–0.6–0.3–0.7–1.3–1.6; mid leg 0.8–0.4–0.4–0.6–1.4–1.6; hind leg 0.8–0.3–0.4–0.7–1.3–1.7; tarsomere 4 of all legs slightly longer than 3 (1.2), tarsomeres 5 all similar, straight, slightly expanded apically; claw sickle-shaped, simple.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; dorsocentral series complete; prescutals several (9–11); supraalars absent; prescutellars several; scutellars very numerous, long and concentrated in group laterally, a few scattered mediad; preepisternals few (5); episternals few (2); metapleurals several (8); suprametapleurals several (6–8).

*Terminalia* (Fig. 73). VIIIth sternite well sclerotized throughout, base slightly narrowed, and ill defined at corners; lateral margin curved and indented slightly at midlength indicating distal origin of lobes; medial depression shallow, very broadly V-shaped, internal sclerotization flat, fusiform; lobe very slightly divergent, apex not closely appressed to hypogynial plate. Hypogynial plate complex, base as broad as lobes, lobe with broad neck, dorsal division short, lobulate, nude, ventral division broad, very weakly denticulate laterally, denticulae becoming better defined mediad. Spermathecae three, moderate-sized, well sclerotized, and with minute clear pits on proximal third; all similar, pear-shaped, with smooth outline, necks short and straight.

Sensilla.—Sternite VIII with 30–40 medium setiforms, distributed generally over lobe.

**Pupa and Larva.** Unknown.

**SPECIMENS EXAMINED.** Types: HOLOTYPE male (terminalia mounted on slide no. CLH 86-602); ALLOTYPE female (terminalia mounted on slide no. CLH 87-145); 13 male and 1 female PARATYPES (partly in alcohol; some terminalia and heads mounted on slides): COLOMBIA, *Antioquia,* Quebrada Salado, 14 Jun 1984, C.L. Hogue, CLH 325 (LACM).

**Additional Specimens.** COLOMBIA, *Antioquia,* Quebrada Alarcona, 22 Jun 1983, C.L. Hogue, CLH 307 (20 males). Quebrada El Salado, 24 km E Santuario, 10 Jan 1986, C.L. Hogue, CLH 353.1 (1 male).

*Valle,* Quebrada Honda, Peñas Blancas, 1,800 m, 3 Jun 1974, C.L. Hogue (1 male, 3 females).

**ETYMOLOGY.** The name is a feminine compound noun in the nominative case transliterated from Greek. It is used in apposition to the generic name and refers to the complete lack of the inner lobe of the dististyle in the male genitalia (Greek *a* = without + *stylis* = stylus).

**REMARKS.** The close relationship of this and *L. lichanos* has been noted above. Variation in the female terminalia make the two species difficult to distinguish on the basis of this set of structures alone. The immatures are not known but are expected to be similar to those of *L. lichanos.*

## 10. *Limonicola davila* Hogue, 1982

Not figured

*Limonicola davila* Hogue, 1982.

**SPECIMENS EXAMINED.** COLOMBIA, *Antioquia,* 49.9 km E Marinilla, 14 Jun 1984, C.L. Hogue, CLH 326 (2 males); 7.6 km W Porce, at km 57, 16 Jun 1984, C.L. Hogue, CLH 332 (4 males, 3 pupae).

**REMARKS.** These records represent an unexpected extension of the range of a species formerly thought to be endemic to the isolated Sierra Nevada de Santa Marta in extreme northern Colombia. *Limonicola davila* may be distinguished from similar species of *Limonicola* by the keys provided above.

## 11. *Limonicola medius* Hogue, new species

Figures 100, 106–110, 114–117

**DIAGNOSIS.** *Adult.*—Externally, males of *L. medius* and *davila* are indistinguishable; the weak pollex on the hind tarsomere 5 is distinctive in the female. The L-shape of the outer gonostylus of the male terminalia is definitive, the much longer ventral lobe giving the structure a V-shape in *L. davila. Pupa.*—The pupa is extremely similar to that of *L. lichanos;* only the excised anterior margin at the base of the anterior lamellar plate and larger bulla at the base of the lamellae distinguish it from that species. *Larva.*—The larva is not known with certainty; it may be very similar and presently indistinguishable from that of *L. lichanos.*

**DESCRIPTION. Male** (Figs. 106, 108). Only one alcoholic specimen available. Very similar to *L. davila. Coloration.* Not available. Wing membrane infuscate. *Size.* A medium-sized blephariceríd. Measurements (N = 1): wing length 3.5. Leg segment lengths:

|  |  | fore leg |
|---|---|---|
|  |  | 1.9 |
| femur |  | 1.4 |
| tibia | 1 | 1.2 |
| tarsus | 2 | 0.51 |
|  | 3 | 0.30 |
|  | 4 | 0.17 |
|  | 5 | 0.22 |

|  |  | mid leg |
|---|---|---|
| femur |  | 1.4 |
| tibia |  | 1.3 |
| tarsus | 1 | 1.1 |
|  | 2 | 0.45 |
|  | 3 | 0.26 |
|  | 4 | 0.16 |
|  | 5 | 0.21 |

|  |  | mid leg |
|---|---|---|
| femur |  | 3.9 |
| tibia |  | 3.7 |
| tarsus | 1 | 1.4 |
|  | 2 | 0.68 |
|  | 3 | 0.43 |
|  | 4 | 0.24 |
|  | 5 | 0.22 |

*Head* (Fig. 106). Colocephalous type, subholoptic. Eyes disjunct dorsally, interocular distance equal to combined width of eight ommatidia. Mouthparts poorly developed, proboscis very short, labium about 0.4 head width, labellar lobes divergent, lobe slightly incurved, bladelike, with acute apex; palpus very short, a single diminutive segment, sensory pit of segment 3 absent, replaced by a single alveoliform. Antenna 15-segmented, flagellar segments moniliform; ultimate segment slightly smaller (0.9) than penultimate, proportions of apical three segments 1.0–1.0–0.9.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: facials—a pair of stout setae high on vertex, one on either side; clypeals few (1); occipitals several (10–11), marginal to eye; postgenals numerous (16–18), long; labrals and labials absent; labellars numerous, long, scattered throughout.

*Thorax and appendages* (Fig. 108). Anal angle of wing produced, lobular. Legs long, slender; fore femur sinuously curved, incrassate; hind legs considerably longer than other legs. Tibial spurs 0–0–1, spur short. Progressive leg segment proportions: fore leg 1.7–0.9–0.4–0.6–0.6–1.3; mid leg 1.0–0.8–0.4–0.6–0.6–1.3; hind leg 1.0–0.4–0.5–0.6–0.6–0.9; tarsomere 4 short in relation to 3 in all legs (0.6). Hind tarsal segments inflated; tarsomeres 5 similar on all legs, curved, with pollex of heavy setae; claw sickle-shaped, with sub-basal tooth.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals few, on anterior part of scutum only; dorsocentral series absent; prescutals and supraalars absent; prescutellars few (1); scutellars numerous, in lateral group, none scattered mediad; preepisternals few (2–3), long; metapleurals numerous (18); suprametapleurals several (7).

*Terminalia* (Figs. 114–117). Cerci slightly divergent; interlobular depression wide, V-shaped; individual cercus subtriangular. Subanal pouch without microtrichia on inner surface. Outer gonostylus moderately large, an elongate, curved strap with a short, ventrobasal lobe. Inner gonostylus a flat prong with angled, rounded apex and broadened base. Anterior lobes of gonites moderately expanded; apodeme small. Sperm sac large. Aedeagal rods moderately long.

Sensilla.—Epandrium with numerous medium setiforms in transverse series. Cercus with medium setiforms generally over apical half; setae of inner arm few but distributed along entire lengths. Outer gonostylus with medium setiforms general over distal half; several moderately long setiforms on inner face dorsobasally. Xth tergite with or without pair of very short setiforms sublaterally. Xth sternite non-setate.

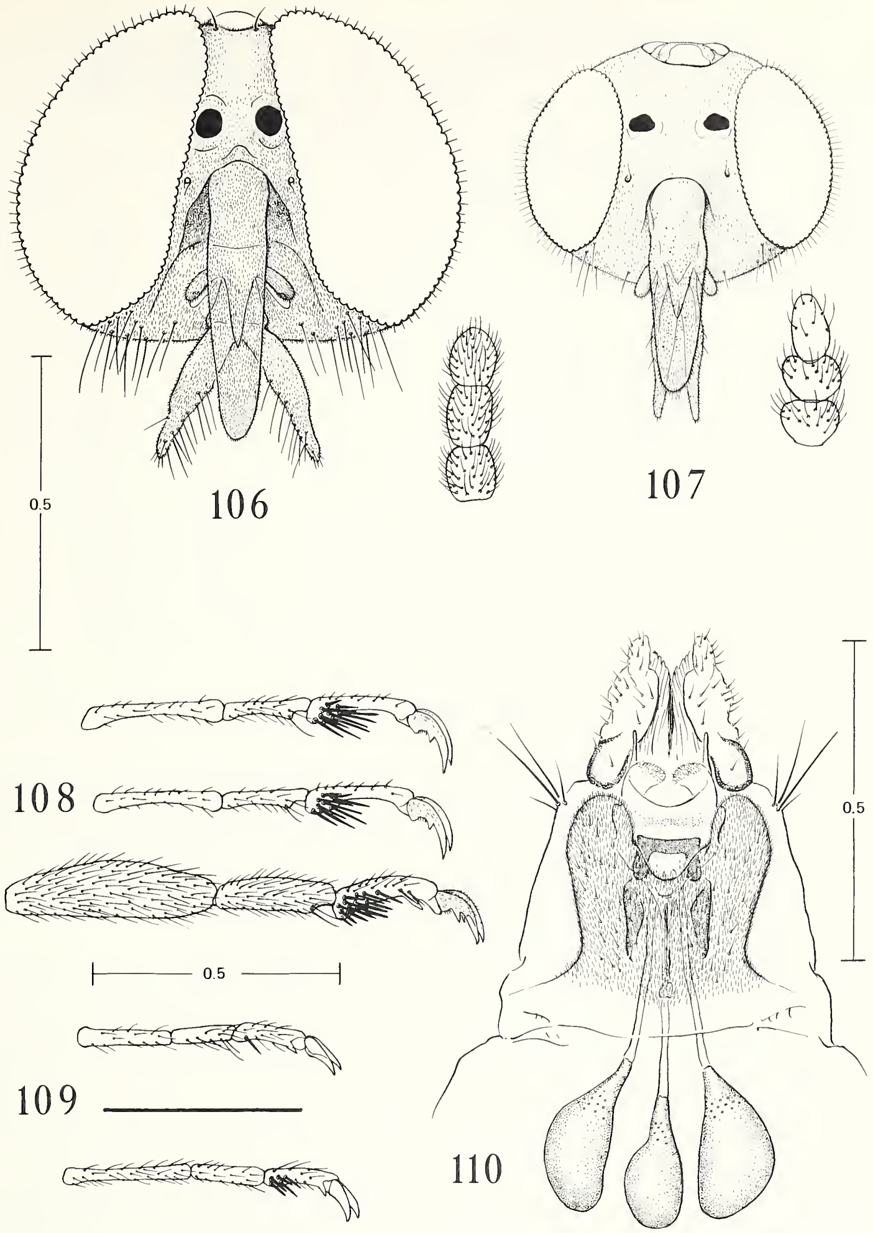
**Female** (Figs. 107, 109, 110). Only one imperfect alcoholic specimen available. Very similar to *L. davila. Coloration.* Not available. Wing membrane infuscate. *Size.* A medium-sized blephariceríd. Measurements (N = 1): wing length 3.8. Leg segment lengths (mid leg unextended and not measurable):

|  |  | fore leg | hind leg |
|---|---|---|---|
| femur |  | 1.0 | 2.3 |
| tibia |  | 1.0 | 2.0 |
| tarsus | 1 | 0.6 | 0.8 |
|  | 2 | 0.31 | 0.41 |
|  | 3 | 0.19 | 0.27 |
|  | 4 | 0.14 | 0.16 |
|  | 5 | 0.16 | 0.16 |

*Head* (Fig. 107). Structure.—Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance 0.33 head width. Mouthparts poorly developed, mandibles and lacinia absent; proboscis very short, labium about 0.5 head width; apex of labrum and hypopharynx acute, margin of latter entire; labellar lobes divergent, lobe straight, bladelike, with acute apex; palpus very short, a single diminutive segment (=segment 3), sensory pit absent, replaced by group of several small alveoliforms. Antenna 15-segmented, flagellar segments moniliform, ultimate segment longer (1.5) than penultimate, proportions of apical three segments 1.0–1.0–1.5.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few (2); occipitals numerous (13); postgenals and labrals absent; labials absent except for a few minute setiforms apically; labellars absent.

*Thorax and appendages* (Fig. 109). Anal angle of wing produced, lobular. Legs moderately long, very slender; fore femur sinuously curved, incrassate; hind legs considerably longer than other legs. Tibial spurs 0–0–1. Progressive leg segment proportions: fore leg 1.0–0.6–0.5–0.6–0.7–1.1; mid leg not available; hind leg 0.9–0.4–0.5–0.7–0.6–1.0; tarsomere 4 short in relation to 3 on all legs (0.6–

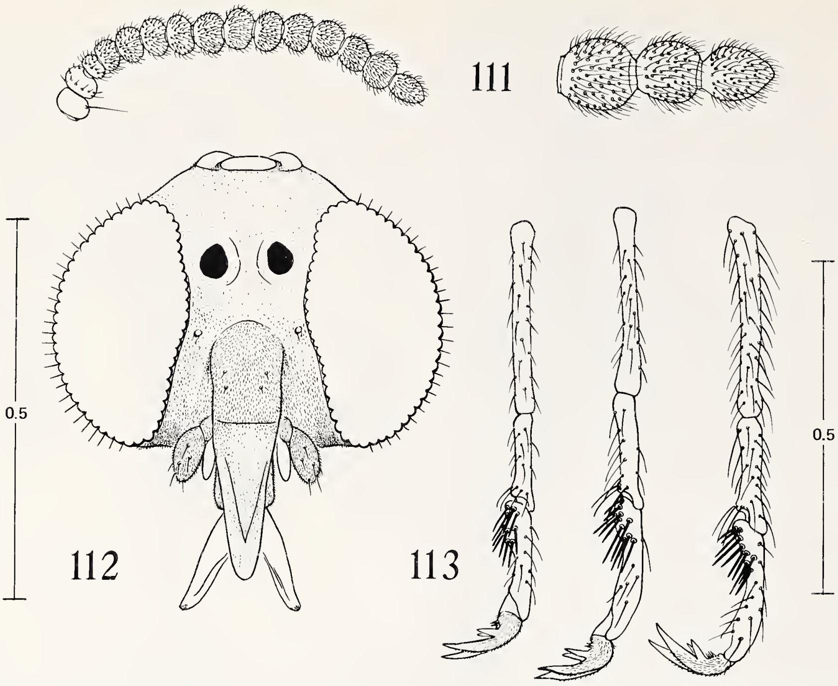


Figures 106–110. *Limonicola medius.* **106.** Male head (frontal view) and terminal antennal segments (inset). **107.** Female head and terminal antennal segments (arrangements as for male). **108.** Terminal tarsal segments of male (fore leg, upper; mid leg, center; hind leg, lower; lateral view). **109.** Terminal tarsal segments of female (arrangement as for male, center not available). **110.** Female terminalia (ventral view).

0.7). Tarsomeres 5 similar on fore and hind legs (mid leg not available), with weak pollex of heavy setae; fore pollex with a single seta, hind pollex with several setae; claw broadly sickle-shaped, simple.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; a few setae in dorsocentral series; prescutals, supraalars, and prescutellars absent; scutellars several to numerous in lateral group, few scattered mediad; preepisternals absent; metapleurals few (5), placed along anterior margin; suprametapleurals few (3–4).

*Terminalia* (Fig. 110). VIIIth sternite well sclerotized throughout, base broad and well defined; lateral margin straight, medial depression shallow, U-shaped, internal sclerotization narrow; apex of lobe produced, broad, angled slightly mediad. Hypogynial plate complex, base as broad as lobes, lobe with broad neck, dorsal division long, fingerlike, ventral division denticulate apically. Spermathecae



**Figures 111–113.** *Limonicola kolomeros.* **111.** Antenna of male. **112.** Male head (frontal view). **113.** Terminal tarsal segments of male (fore leg, left; mid leg, center; hind leg, right; lateral view).

three, moderate-sized, well sclerotized, all similar, pear-shaped, with smooth outline, one smaller than others, necks short and straight.

Sensilla.—Sternite VIII with 27–29 medium setiforms, distributed generally over lobe.

**Pupa** (Fig. 100). *Integument.* Periphery abrupt, sclerotized ventral border present. Papillose dorsally. Papillae even and very dense generally (individual papillae nearly contiguous). Individual papillae subequal, small; smooth, rounded, oval convexities. Papillar distribution as follows: scutum—dense over entire disc; branchial sclerite—dense over entire surface; metathoracic sclerite—even and dense over entire surface; abdominal tergites—even and dense except for medial bosses where they are denser.

*Size.* Small for family. Measurements, male (N = 2): body length 3.9 (3.8–4.0), width 2.6 (2.6–2.6); female pupa unknown.

*Structure.* Outline shape ovoid, thorax abruptly narrowed, more so in male than female. L/W male = 1.5, female unknown. Cross section obtuse subtriangular, upper sides moderately inclined. Dorsal sclerites: cephalic sclerite irregular, with slight paramedial convexities. Branchial sclerite longer than tall, smoothly rounded and not projecting beyond cephalic sclerite. Anterior margin of scutum moderately inclined, not lobed. Suture separating metathoracic sclerite from abdominal tergite I V-shaped medially. Abdominal tergites with slight, anteromedial bosses; lateral margins entire.

*Branchiae.* Large, erect, anterior plates divergent, middle and posterior plates parallel. Outer plates subtriangular, elongate, broadly rounded apically; inner plates strap-shaped, much narrower than outer and slightly longer (exerted); outer margin of anterior plate excavate basally; anterior plate expanded posterobasally to form a large, conspicuous, spherical bulla.

**Larva.** Unknown.

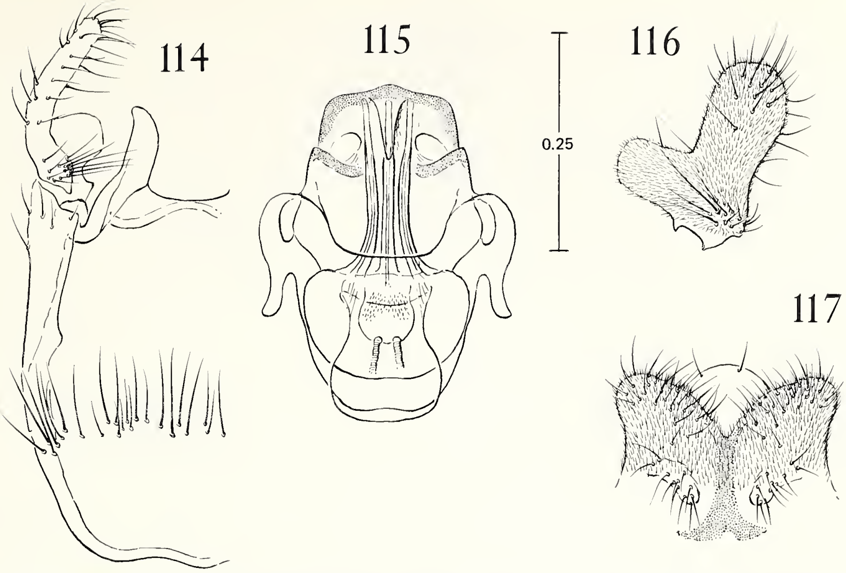
**SPECIMENS EXAMINED.** Types: HOLOTYPE male (alcoholic specimen dissected and mounted on slides nos. CLH 88-4H, 88-4B, 88-4W, and 87-159); ALLOTYPE female (alcoholic specimen dissected and mounted on slides nos. CLH 88-5H, 88-5B, 88-5W, and 87-160: COLOMBIA, *Antioquia*, Quebrada Alarcona, 22 Jun 1983, C.L. Hogue, CLH 307 (LACM).

**Additional Specimens.** COLOMBIA, *Antioquia*, Quebrada La Agudelo, 2.5 km S El Retiro, 10 Jun 1984, C.L. Hogue, CLH 319 (8 pupae).

**ETYMOLOGY.** The name is the masculine form of the Latin adjective *medius,* meaning central, intermediate, or neutral, in reference to the species' similarities to both *L. lichanos* and *L. davila.*

**REMARKS.** The partially developed ventrobasal lobe of the dististyle places this species in an intermediate position between *L. lichanos* and *L. davila.* The pupa is similar to that of *L. lichanos,* i.e., with a middorsal ridge. The convexities in the pupa of that species are associated with the central bosses of the abdominal segments, so the larva of *L. medius* could be of the *L. lichanos* type.

The pupa and adults are associated by the ontogenetic method. Some larvae (not recorded as Specimens Examined) were collected with the pu-



**Figures 114–117.** *Limonicola medius,* male terminalia (dorsal views). **114.** Genital capsule and gonostyli. **115.** Mesosomal structures and gonites. **116.** Left outer gonostylus (inner view). **117.** Cercal complex.

pae (Quebrada La Agudela) and these appear to be *L. lichanos,* with central bosses on the abdominal segments. Because the pupae exhibit central convexities on the dorsa of the abdominal tergites, the larvae may be conspecific and represent this stage of *L. medius.* It is preferable not to make this assumption (using the unreliable syntopic method) until additional material becomes available.

## 12. *Limonicola kolomeros* Hogue, new species

Figures 111–113, 118–121

**DIAGNOSIS.** *Adult.* This species is distinguished by the reduced first and second flagellar segments in the antenna, a condition known in no other member of the genus. The subtriangular outer gonostylus is unique also, as is the inner gonostylus (bifurcate, with broadly rounded sublobes). The female and immatures are unknown.

**DESCRIPTION. Male** (Figs. 111–113, 118–121). Only alcoholic and slide mounted specimens are available. *Coloration.* Not available. Wing membrane infuscate. *Size.* A medium-sized blepharicerid. Measurements (N = 4): wing length 3.4 (3.3–3.5). Leg segment lengths:

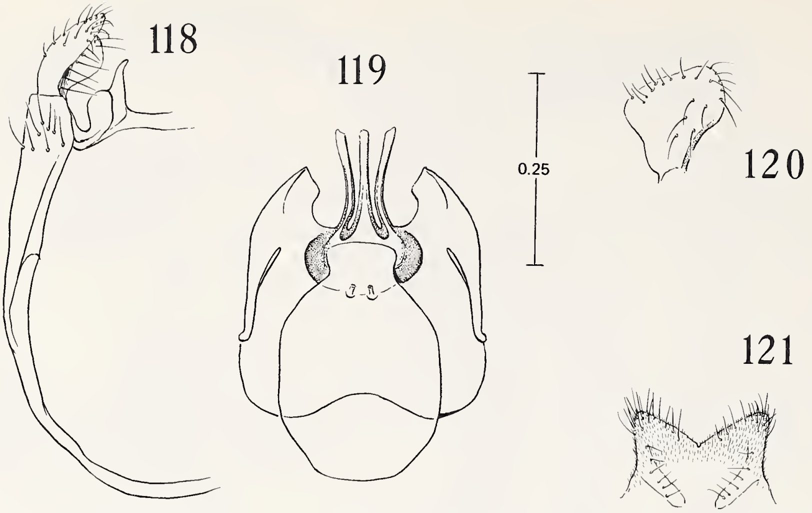
| | | fore leg |
|---|---|---|
| femur | | 1.2 (1.1–1.3) |
| tibia | | 1.4 (1.3–1.4) |
| tarsus | 1 | 0.9 (0.8–1.0) |
| | 2 | 0.46 (0.42–0.52) |
| | 3 | 0.29 (0.27–0.32) |
| | 4 | 0.16 (0.14–0.18) |
| | 5 | 0.21 (0.19–0.22) |

| | | mid leg |
|---|---|---|
| femur | | 1.6 (1.5–1.7) |
| tibia | | 1.4 (1.3–1.4) |
| tarsus | 1 | 0.8 (0.8–0.9) |
| | 2 | 0.47 (0.45–0.53) |
| | 3 | 0.30 (0.28–0.33) |
| | 4 | 0.17 (0.16–0.19) |
| | 5 | 0.21 (0.21–0.21) |

| | | hind leg |
|---|---|---|
| femur | | 3.0 (2.6–3.6) |
| tibia | | 2.9 (2.5–3.5) |
| tarsus | 1 | 1.0 (0.9–1.1) |
| | 2 | 0.55 (0.50–0.63) |
| | 3 | 0.34 (0.30–0.38) |
| | 4 | 0.19 (0.17–0.20) |
| | 5 | 0.21 (0.21–0.22) |

*Head* (Figs. 111, 112). Colocephalous type, dichoptic. Eyes distant dorsally, interocular distance 0.3 head width. Mouthparts poorly developed, proboscis very short, labium about 0.4 head width, labellar lobes long (1.6 length of labium), divergent, lobe straight, bladelike, with rounded apex; palpus very short, a single diminutive segment, sensory pit absent, replaced by group of several small alveoliforms. Antenna 15-segmented, flagellar segments moniliform, flagellar segments 1 and 2 compressed and slightly smaller than more distal segments; ultimate segment subequal to penultimate, pear-shaped, proportions of apical three segments 1.0–1.0–1.0.

Sensilla.—Setiform groups on head capsule and mouthparts as follows: clypeals few (0–4); occipitals numerous (14–22); postgenals absent; labrals and labials absent; labellars absent except for a few minute setiforms apically.



**Figures 118–121.** *Limonicola kolomeros,* male terminalia (dorsal views). **118.** Genital capsule and gonostyli. **119.** Mesosomal structures and gonites. **120.** Left outer gonostylus (inner view). **121.** Cercal complex.

*Thorax and appendages* (Fig. 113). Anal angle of wing produced, lobular. Legs moderately long, very slender; fore femur sinuously curved, slightly incrassate; hind legs considerably longer than other legs. Tibial spurs 0–0–0. Progressive leg segment proportions: fore leg 1.2–0.7–0.5–0.6–0.6–1.3; mid leg 0.9–0.6–0.6–0.6–0.6–1.3; hind leg 1.0–0.4–0.6–0.6–0.6–1.1; tarsomere 4 short in relation to 3 in all legs (0.6). Hind tibia and tarsus slender throughout, no segments or portions inflated; tarsomeres 5 similar on all legs, curved, with pollex of heavy setae; claw sickle-shaped, with sub-basal tooth and 3–4 small denticulae between base and tooth.

Sensilla.—Setiform groups on thoracic sclerites as follows: acrostichals absent; dorsocentral series complete; prescutals few (5); supraalars in two groups: far dorsal group few (3–6), ventral group few to several (4–6); prescutellars few, scattered; scutellars several in lateral group, few scattered mediad; preepisternals few (1–2); metapleurals few (4); suprametapleurals few (4).

*Terminalia* (Figs. 118–121). From two imperfect specimens. Cerci and interlobular depression indeterminate. Subanal pouch without microtrichia on inner walls. Outer gonostylus medium-sized, a rounded triangle formed from an expanded ventral margin midventrally. Inner gonostylus bifurcate, unequal sublobes broadly rounded apically. Anterior lobes of gonites (ventral bridge) greatly expanded; apodeme expansive. Sperm sac very small. Aedeagal rods very short.

Sensilla.—Epandrium with numerous medium setiforms in a transverse series. Setae of cercus indeterminate. Setae of inner arm few and distributed along entire length. Outer gonostylus with medium setiforms generally distributed on distal half; no basal group on inner surface. Setae of Xth tergite and sternite indeterminable.

**Female, Pupa, and Larva.** Unknown.

**SPECIMENS EXAMINED.** HOLOTYPE male (alcoholic specimen dissected and mounted on slides nos. CLH 87-214, 87-214W, 87-214B, and 87-214H; 3 PARATYPE males (two in alcohol, one dissected and mounted on slides nos. CLH 87-213, 87-213W, 87-213B, and 87-213H): COLOMBIA, *Antioquia,* Quebrada Alarcona, 22 Jun 1983, C.L. Hogue, CLH 307 (LACM).

**ETYMOLOGY.** The name is a masculine compound noun in the nominative case taken directly from Greek and used in apposition to the generic name; it refers to the reduced size and compression of the basal flagellar segments in the male antenna (Greek *kolos* = stunted + *meros* = segment).

**REMARKS.** This species is very poorly known, being represented by only four adult male specimens. It is a distinctive species, however, unlike other *Limonicola* in the compression of antennal flagellar segments and characteristics of the terminalia, especially the very small sperm sac and other features given above.

## 13. *Limonicola* unidentified larva 1

Figures 122, 124

*Limonicola* sp. 2 of Bedoya, 1984. Bedoya and Roldán, 1984:118, fig. 4c. Roldán, 1988: fig. 142.

**DESCRIPTION. Larva** (Figs. 122, 124). *General.* Body form lobiform. Outline shape of anterior division multiangular, roughly hexagonal.

*Integument.* Dorsum lightly sclerotized. Corrugations distinct, fine and irregular. Venter with a moderate-sized (not extending anterior to base of pseudopod), oval patch of denticulae at bases of pseudopods.

*Coloration.* Trunk pigmentation even, light

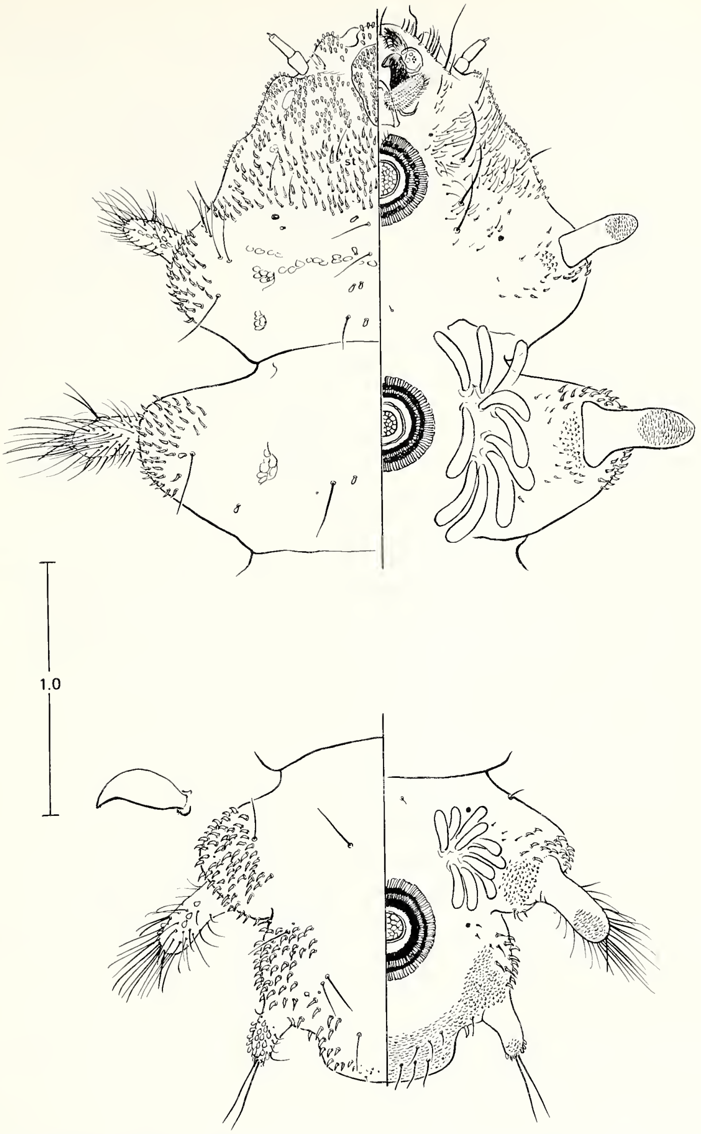


**Figure 122.** *Limonicola* unidentified larva 1 (dorsal view, left; ventral view, right; typical modified sensillum, inset).

brown; sclerotized portions pale brown; terminal border unpigmented.

*Size.* Medium for the family. Measurements (N = 10): body length 6.8 (5.2–8.7), head capsule width 1.5 (1.2–1.8), antennal segment lengths, basal 0.07 (0.06–0.08), apical 0.14 (0.11–0.18).

*Head.* Antennal segment proportions 1.0–2.0.

*Trunk.* Dorsum evenly rounded, without convexities, projections or special sclerotizations.

*Anal division.* Dorsal pseudopod a moderately large, elongate lobe, directed posterolaterad. Terminal incision U-shaped, spacious. Terminal lobe narrowed posteriad, with convex, posterior margin.

*Primary sensilla* (medium setiforms unless otherwise described). tM–T in line, well spaced; tI–VI often double; inner tpP anteromedial to spiracle. Outer tpI–VI indiscernible. Terminal setae 3–3, small, sub-marginal, inserted ventrally.

*Dorsal modified sensilla.* Dense large ascinaciforms on medial head sclerites; smaller, curved, obovate types on lateralia. Ascinaciforms laterally only on abdominal segments I–VIII, curving ventrad around base of pseudopods. Dorsal sensilla of pseudopods mostly setiform, a few curved, oviform types intermingled, latter dominant on dorsal pseudopod of segment VII. Integument set with general background field of small, fine setiforms.

**SPECIMENS EXAMINED.** COLOMBIA, *Antioquia,* Quebrada Alarcona, 22 Jun 1983, C.L. Hogue, CLH 307 (3 larvae). Quebrada La Agudelo, 2.3 km S El Retiro, 10 Jun 1984, C.L. Hogue, CLH 319 (1 larva).

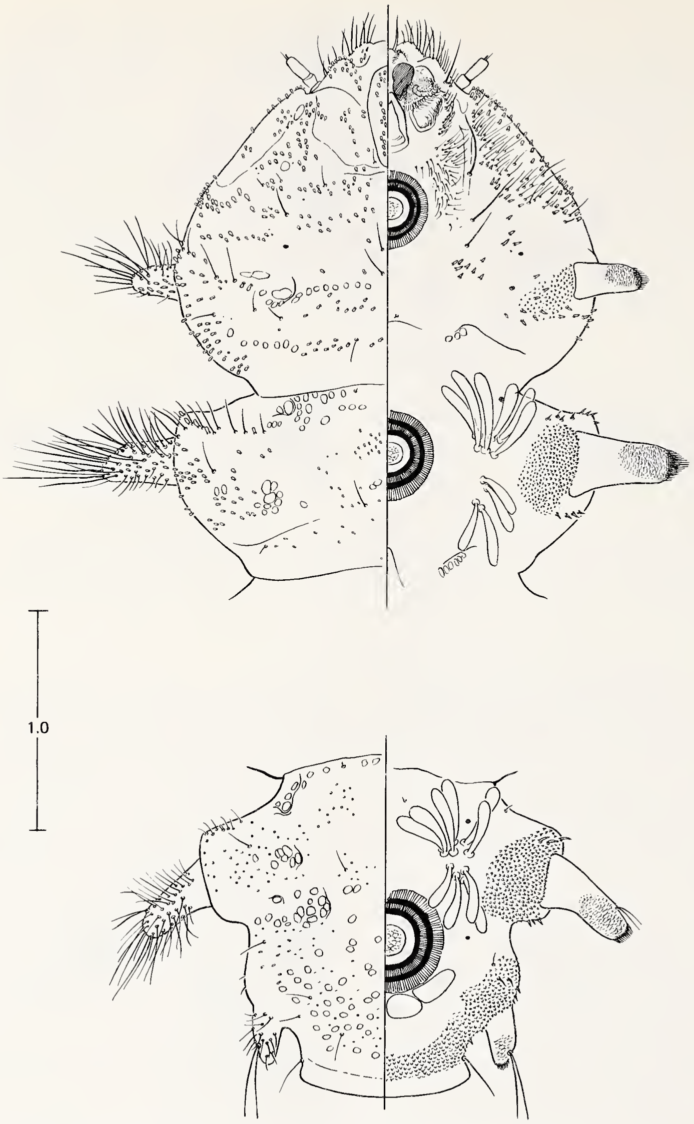


**Figure 123.** *Limonicola* unidentified larva 2 (dorsal view, left; ventral view, right).

*Quindio,* Rio Quindio, 10 km N Armenia, Boquia, 18 Jun 1984, C.L. Hogue, CLH 337 (1 larva). *Valle,* Quebrada Honda, Peñas Blancas, 1,800 m, 3 Jun 1974, C.L. Hogue (10 larvae).

**REMARKS.** The larva is very different from any other in Antioquia Department; the conspicuous ascinaciform dorsal sensilla are unique. We have no clue as to its identity.

## 14. *Limonicola* unidentified larva 2

Figures 123, 125

**DESCRIPTION. Larva** (Figs. 123, 125). *General.*—Body lobiform. Outline shape of anterior division subovate.

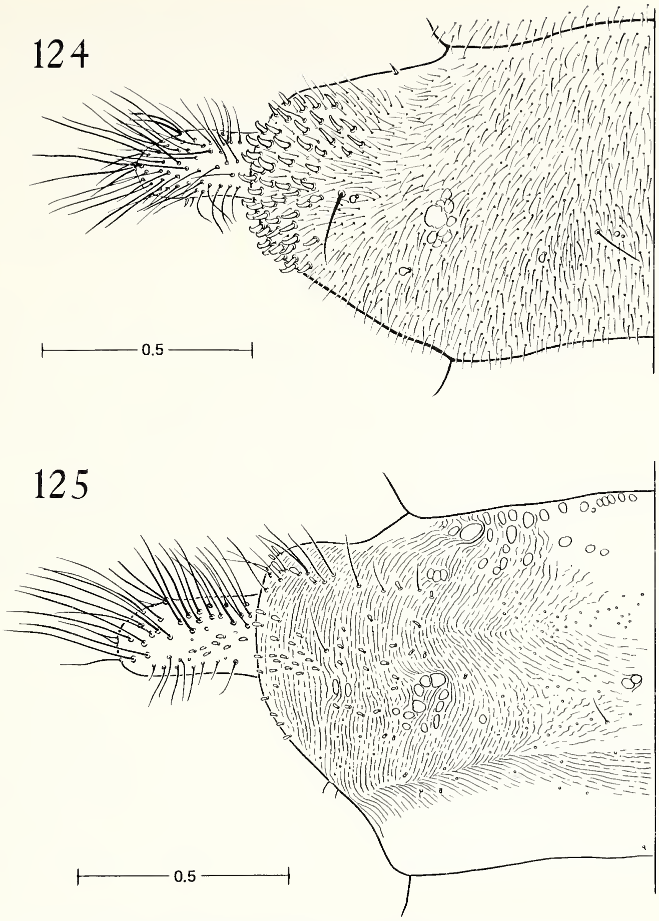
*Integument.* Dorsum moderately well sclerotized. Corrugations of integument distinct, fine, linear to zig-zagging, linear ones convergent over anterior and posterior transverse ridges. Venter with an extensive (extending anterior to base of pseudopod), oval patch of strong denticulae at bases of pseudopods.

*Coloration.* Trunk pigmentation even; sclerotized portions pale brown, terminal border thick, sclerotized, black.

*Size.* Medium for the family. Measurements (N = 10): body length 6.4 (6.1–6.7), head capsule width 1.4 (1.3–1.5), antennal segment lengths, basal 0.05 (0.05–0.07), apical 0.12 (0.11–0.13).

*Head.* Antennal segment proportions 1.0–2.3.

*Trunk.* Dorsum evenly rounded, without convexities or projections; numerous small, oval plates on anal division.



**Figures 124, 125.** *Limonicola* larvae, abdominal segment III (left half, dorsal view). **124.** *L.* unidentified larva 1. **125.** *L.* unidentified larva 2.

*Anal division.* Dorsal pseudopod moderately large, an elongate lobe, directed posteriad. Terminal incision asymmetrically U-shaped, narrow. Terminal lobe truncate, posterior margin slightly arcuate, lateral corners often slightly produced.

*Primary sensilla* (medium setiforms unless otherwise described). tM-T in line, well spaced. Inner tpP anterior to spiracle. Outer tpI-VI indiscernible. Normal terminal setae absent, a large, conspicuous, setiform present on the lateral edge of the terminal border.

*Dorsal modified sensilla.* Sparse, small pyriforms on head sclerites. Trunk integument generally with a few sparse, minute setiforms/pyriforms, these larger and linearly arranged anterolaterally, forming a series curving ventrad around base of pseudopod. Dorsal sensilla of pseudopods all long setiform. Background field of small setiforms absent.

**SPECIMENS EXAMINED.** COLOMBIA, *Antioquia,* Aug 1983, I. Bedoya, 6 (6 larvae). Salto Tequendamita, 23 Jun 1983, C.L. Hogue, CLH 310 (15 larvae). Quebrada Iguaná, 13 Jun 1984, C.L. Hogue, CLH 323 (4 larvae). Quebrada La Cascada, 13 Jun 1984, C.L. Hogue, CLH 324 (118 larvae). Quebrada Piedra Blanca, 12 km W Guarne, 8 Jan 1986, C.L. Hogue, CLH 347.1.1, 347.3.1 (104 larvae). Quebrada La Cascada, 9.1 km E Medellín, 23 Jun 1983, C.L. Hogue, CLH 309.3 (33 larvae). 1 km SE Paso de Boquerón, 22 Jun 1983, C.L. Hogue, CLH 300 (13 larvae). Quebrada La Hundida, 16.8 km E Santuario, 8 Jan 1986, C.L. Hogue, CLH 348.2 (7 larvae). Quebrada Tebaida, 52.4 km E Santuario, 10 Jan 1986, C.L. Hogue, CLH 352.1 (6 larvae).

*Valle,* Quebrada Honda, Peñas Blancas, 1,800 m, 3 Jun 1974, C.L. Hogue (1 larva).

**REMARKS.** The isolated setae situated at the outer corners of the terminal lobe distinguish this larva from all others. Its similarity otherwise to the larva of *L. davila* suggests its possible identity to the similar *L. medius* or *L. astylis,* but no material is available to confirm this speculation.

## NOTES ON ECOLOGY

As elsewhere in the Neotropics, the Blephariceridae of Antioquia show a fairly narrow range of adaptations to cool, clean, well-oxygenated, erosional

Table 1. Numbers in box indicate times species pairs occurred at same collection locality.

| | P. roldani | P. aspergonympha | P. charadrae | P. eldorado | P. saltana ? | P. inca | P. andeana | L. lichanos | L. astylis | L. davila | L. subdavila | L. kolomeros | L. unid. larva 1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P. aspergonympha | 1 | | | | | | | | | | | | |
| P. charadrae | 3 | 1 | | | | | | | | | | | |
| P. eldorado | 1 | | | | | | | | | | | | |
| P. saltana ? | | | | | | | | | | | | | |
| P. inca | 2 | | | | | | | | | | | | |
| P andeana | 2 | | 1 | | | | | | | | | | |
| L. lichanos | 2 | | 1 | | | | 1 | | | | | | |
| L. astylis | 2 | | 1 | | | 1 | | 1 | | | | | |
| L. davila | | | | | | | | | | | | | |
| L. subdavila | | | | | | | | | 1 | | | | |
| L. kolomeros | | | | | | | | | 1 | | 1 | | |
| L. unid. larva 1 | 1 | | | | | 1 | | 1 | | | 1 | | |
| L. unid. larva 2 | 5 | | 1 | 2 | | 1 | 2 | 1 | 1 | | | | 1 |

streams. Immatures were found in water with temperatures ranging from 13 to 28 degrees centigrade; pH was near neutrality to slightly alkaline (pH 6.6–8.4); a high percent saturation of oxygen (90–112%); low concentrations of dissolved ions (conductivity $\mu$mhos/cm$^2$ 20–60). The elevations at which blephariceridswere collected ranged from 500 to 2,500 m above sea level.

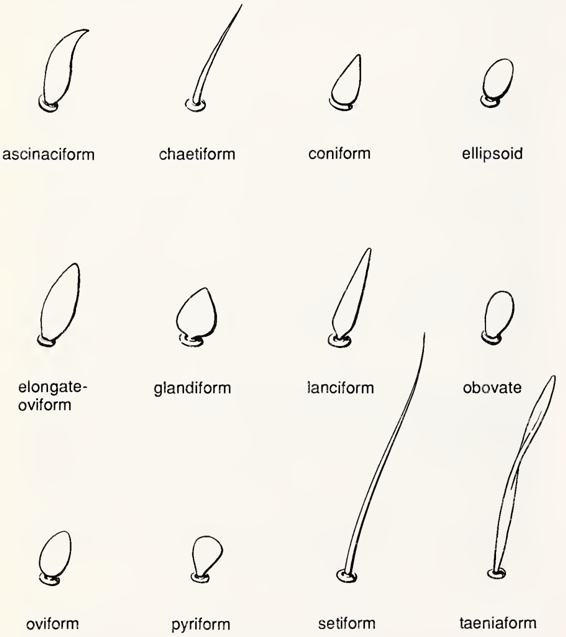


**Figure 126.** Explanation of terms used to describe the various forms taken by the specialized dorsal sensilla of blepharicerid larvae.

Most species occurred in isolation at collection sites; several were associated with at least one other, some with several, species. Closely related and distantly related species were found inhabiting the same stream sectors. See Table 1 for a summary of species' associations.

As Hogue has found in his general collecting in Antioquia, *Limonicola* larvae and pupae tend to occupy smaller, free stones and be totally submerged; *Paltostoma* is more inclined to live at or just below the water surface, on larger rocks that are embedded in the substrate.

## ACKNOWLEDGMENTS

A number of individuals and agencies made it possible for us to realize our fieldwork leading to the accumulation of material upon which this paper is based. In particular we are indebted to Dr. Gabriel Roldán Pérez, Chairman, Graduate Biology Program, Universidad de Antioquia, Medellín, Colombia, for his central role in providing guidance and substantive support. The facilities of the Limnology Laboratory Alexander von Humboldt, also under the direction of Dr. Roldán, were in a significant measure made available through the generosity of the Alexander von Humboldt Foundation, Bonn, Federal Republic of Germany. Funds from the Los Angeles County Museum of Natural History Foundation and University of California Extension made possible much of Hogue's travel. The majority of the project was supported by a grant to Hogue from the Systematic Biology Program of the U.S. National Science Foundation (BSR 8415044).

To our friends and collegues who helped in many aspects of progress we also express our thanks and appreciation; they include Uwe Matthias, Gil Challet, Margarita Correa, Marta Wolf, and Luis Fernando Roldán.

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## LATE CENOZOIC LIZARDS OF THE ANZA BORREGO DESERT, CALIFORNIA

MARK A. NORELL

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# LATE CENOZOIC LIZARDS OF THE ANZA BORREGO DESERT, CALIFORNIA

MARK A. NORELL[1]

**ABSTRACT.** Late Neogene (Blancan and Irvingtonian) deposits from the Palm Springs Formation in Anza Borrego State Park (San Diego County, California, U.S.A.) have yielded the most diverse Tertiary lizard assemblage yet reported. Five lizard families are represented: Iguanidae, Xantusiidae, Scincidae, Teiidae, and Anguidae. The assemblages are taxonomically dominated by the Iguanidae, including *Gambelia corona* n. sp., *Dipsosaurus dorsalis, Pumilia novaceki** n. gen. *et* sp., which is the sister-taxon of *Iguana, Phrynosoma anzaense* n. sp., and two sceloporines not presently referable to genus. The morphology of the fossil *Dipsosaurus dorsalis* suggests that specimens of *Leiocephalus* described from the Neogene of continental North America may be referred to *Dipsosaurus dorsalis.* A new species of xantusiid, *Xantusia downsi**, is described. Several specimens, including all anguids and teiids, could be diagnosed to only general hierarchical levels.

Temporal faunal change took place during deposition of the Palm Springs Formation. Whereas the underrepresentation of some taxa in the lower part of the section may be due to sampling inconsistencies, the disappearance of the iguanine lineages roughly correlates with mammalian faunal turnover events.

The sparse fossil record of Neogene lizards hinders comparison among assemblages. In North America, other late Tertiary lizard assemblages are depauperate, consisting of a skink, a gerrhonotine, and one or two sceloporines. The Anza Borrego stratigraphic sequence contains all of these groups and additional taxa, making it the best indicator of late Tertiary lizard diversity yet surveyed.

**SUMARIO.** Los depósitos del período neogeno tardío (Blancano e Irvingtoniano) de la formación en Palm Springs en el Parque Estatal de Anza Borrego (en el condano de San Diego, California) han provisto los ejemplares más diversos hasta ahora recogidos de las lagartijas del período terciario. Aqui se encuentran cinco familias de lagartijas: los Iguanidae, los Xantusiidae, los Scincidae, los Teiidae y los Anguidae. La fauna está taxónomicamente dominada por los Iguanidae; estos incluyen *Gambelia corona* nueva especie, *Dipsosaurus dorsalis,* un nuevo género *Pumilia novaceki**, que se el groupo hermano al de los *Iguana, Phrynosoma anzaense* nueva especie y dos sceloporines a los cuales por el momento no se puede aludir como a un género. La morfología del *Dipsosaurus* indica que los especímenes del *Leiocephalus,* hasta ahora descritos como pertenecientes al neogeno de América del Norte continental, pueden referirse como del *Dipsosaurus dorsalis.* Un nuevo especie de Xantusiidae, *Xantusia downsi**, es descrito. Varios especímenes, inclusive todos los anguids y los teiids podrían ser únicamente definidos en niveles jerárquicos generales.

Algún cambio temporal en la fauna ocurrió durante el depósito de la Formación Palm Springs. Aunque la subrepresentación de alguna taxa en la parte inferior de la sección se deba a inconsistencias en la recaudación de ejemplares, la desaparición de los lineajes de Iguanine se puede relacionar con los eventos que transformaron la fauna mamífera.

Los escasos registros de fósiles de lagartijas del neogeno impide la comparación entre faunas. Otras faunas de lagartijas del periódo terciario son por lo general bastante pobres; consisten en un escinco, y un gerrhonotine y uno o dos sceloporines. La fauna en Anza Borrego contiens todas estas formas y otras taxas adicionales, convirtiéndola en el mejor indicador de variedades de lagartijas del período Terciaro que se haya investigado.

## INTRODUCTION

Lizards of the North American southwestern deserts form a characteristic assemblage of taxa that is an important element of the modern fauna of the region. All extant families of North American lizards are present in the region except Amphisbaenidae and Xenosauridae. Regional fossil and modern lizard assemblages are dominated by the taxonomically diverse Iguanidae. Little is known, however, of the history of the modern fauna.

Neogene lizard fossils are rare in southwestern North American fossil deposits. Only a few localities (Lindsay, 1972; Whistler, 1984; Harrison, 1972; Rogers, 1976; and others) have produced representative samples of fossil lizards, and many of these lack accompanying mammalian faunas and tight

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[1] Department of Vertebrate Paleontology, American Museum of Natural History, 79th St. at Central Park West, New York, New York 10024.

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**Table 1.** Faunal list of lizard taxa from the Palm Springs Formation.

- Iguanidae
  - *Dipsosaurus dorsalis*
  - *Pumilia novaceki** n. gen. *et* metasp.
  - *Phrynosoma anazaense* n. sp.
  - *Phrynosoma* sp.
  - Sceloporine Type A
  - Sceloporine Type B
  - *Gambelia corona* n. sp.
- Teiidae
  - *Ameiva/Cnemidophorus*
  - Teiini (basal)
- Xantusiidae
  - *Xantusia downsi** n. metasp.
- Scincidae
  - *Eumeces* sp.
- Anguidae
  - Gerrhonotinae indet.

stratigraphic control, or are represented by very fragmentary specimens. The presence of many lizard fossils from the Vellacito Badlands of Anza Borrego Desert State Park, San Diego County, California (Fig. 1), offers an exceptional opportunity to reconstruct Late Cenozoic regional lizard assemblages (Table 1).

Material used in this study was collected by field parties of the Natural History Museum of Los Angeles County, under the direction of Theodore Downs, from 1957 to the present. The fossil producing areas were originally prospected by Harley J. Garbani. Over 450 fossil localities have been collected through 4000 m of conformable sediments. The localities are stratigraphically tied to the type section of the Palm Springs Formation, which has been paleomagnetically correlated with the magnetic polarity timescale (Opdyke *et al.*, 1977).

Published work on the region's fossil assemblages has been incomplete. Downs and White (1968) reported the initial faunal list for the deposits documenting the rich mammalian fossils. Other reports have dealt with mammalian biostratigraphy (Opdyke *et al.*, 1977), species of the pocket gopher *Geomys* (White and Downs, 1961; Becker and White, 1981), the nyctophyline bat *Anzanycterus anzaense* (White, 1969), and birds (Howard, 1963). Brattstrom (1961) provided the only account of the area's fossil herpetofauna in describing turtle plates as "referable to large tortoises." Previous to the present study, these same lizard specimens were studied by Richard Etheridge, George Callison, and Floyd Richey.

## MATERIALS AND METHODS

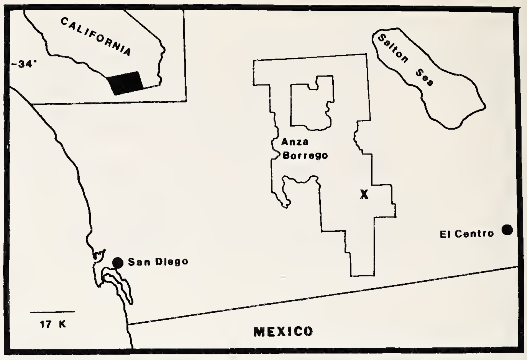

**Figure 1.** Location of Anza Borrego Desert State Park. Area of outcrops marked by an X.

Approximately 75 lizard specimens are catalogued into 75 numbered lots. Locality information is recorded by a number followed by a slash and the specimen number (locality number/specimen number). Stratigraphic position is fixed by "zone" numbers assigned to all fossil-producing localities, in reference to the type section. These zones refer to section thickness and are unrelated to section completeness (*sensu* Schindel, 1980) or faunal composition.

The use of metataxa (signified by an * following the Linnean binomial) follows that of Gauthier *et al.* (1988) as modified from Gauthier (1984), Donoghue (1985), and Mishler and Brandon (1987). Simply, a metataxon is a systematic unit whose monophyly is not established but contains some systematic information. Metataxa designate "suspect or unknown groups that can be considered separately as a general category of uncertain status. This includes unresolved groups for which there is no character evidence demonstrating that they are either monophyletic or paraphyletic" (Gauthier *et al.*, 1988). As used here, metataxa are specimens or groups of specimens that have apomorphic characters linking them with a monophyletic group; however, they lack unique apomorphic characters defining their monophyly. Metataxa display the character condition of an ancestor and their monophyletic sister-group; however, metataxa are not considered as ancestors here for reasons outlined in Schoch (1986) and Gaffney (1979). Because metataxa are recognized by branching pattern and represent the finest level of cladistic analysis, I use this convention only for metaspecies. Because species are the only natural units that can possibly be ancestral, metataxa may in some cases be more than phylogenetic artifacts. Recognition of metataxa at levels higher than the species is not recommended because these groups are of dubious monophyly.

Identification of fragmentary specimens at low taxonomic levels is problematic and often cannot be defended by reference to observable character states. Overinterpretation of the fossil record can lead to problems in analyzing temporal evolutionary and biogeographic patterns. If alpha-level systematics is used as a database for such studies, referral can only be made on the basis of derived characters (synapomorphies). The degree of hierarchical relationship specified for particular specimens is limited by the hierarchical level defined by characters preserved on each specimen. To allow maximum resolution, a hierarchical distribution of diagnostic characters must be established and used in diagnoses. This is especially the case when taxa have been diagnosed elsewhere on the basis of characters not preserved on the fossil specimens. Unfortunately, few lizard families have been analyzed cladistically to lower levels. Where such information is not available, systematic decisions must be conservative.

In naming new taxa, I follow Gauthier *et al.* (1988), who suggest that taxonomic stability can be enhanced if widely used names are "restricted to clades in which at least two branches stemming from the basal node are represented by extant organisms." This approach renders the diagnoses of extant groups immune to change brought about by the description of new fossil material. For instance, *Pumilia novaceki** new genus and metaspecies, although very similar and closely related to species of the genus *Iguana* Laurenti, 1768, would require the rediagnosis of the extant genus *Iguana* if it were included therein. Such redefinition based on often fragmentary fossil material is less informative than diagnoses based on extant material, because it explains less information (*i.e.* character data). For the purpose of maximizing explanatory information and enhancing nomenclatural stability of commonly used names, the suggestions of Gauthier *et al.* (1988) are adopted herein. The taxonomy follows Estes (1983).

## GEOLOGY

The Palm Springs Formation (Woodring, 1931) is exposed in the extensive Vallecito Badlands in the southern section of Anza Borrego Desert State Park. It is a thick unit (approximately 4000 m) that contains over 30 localities that have produced lizard fossils. The Palm Springs Formation is comformably overlain by the younger Canebrake Formation, a granitic gravel and boulder fanglomerate, and underlain by the older Imperial Formation, a predominantly marine unit composed of mud and sandstones with occasional biostromal oyster beds (Pappajohn, 1980). The Palm Springs Formation can be divided into four lithostratigraphic members, each indicative of a different regional depositional environment and varied source terrain. No lizard fossils are known from the conformable underlying marine Imperial Formation, although mammalian remains have been reported (Opdyke *et al.*, 1977).

Sediment composition varies both vertically and regionally. The presence of detrital Cretaceous foraminifera (Merriam and Bandy, 1965) indicates that some of the sediments, especially those lower in the section at the southeastern end of the park, were deposited by the ancestral Colorado River. Up-section and to the north, coarser materials derived from the rising Peninsular and Coast ranges to the west begin to replace the fluvial deposits. The sporadic presence throughout the section of an impoverished marine fauna indicates periodic intrusion of the Gulf of California into the area (Downs and Woodard, 1961).

Based on mammalian faunal associations, Downs and White (1968) divided the fossiliferous section into three local faunal zones independent of lithology. A lower Layer Cake local fauna has characteristic early Blancan affinities, the temporally intermediate Arroyo Seco local fauna is late Blancan in age, and the Vallecito Creek local fauna is late Blancan and early Irvingtonian. Age determination of the Palm Springs sediments has been further refined by magnetostratigraphy (Opdyke *et al.*, 1977; Johnson *et al.*, 1983) (Fig. 2). The magnetic and paleontologic data gave slightly different results, indicating that the Layer Cake local fauna is Early Pliocene (early to middle Blancan), the Arroyo Seco local fauna is Middle Pliocene (middle Blancan), and the Vallecito Creek local fauna is Late Pliocene to Early Pleistocene (late Blancan to early Irvingtonian) (Downs, pers. comm., 1985).

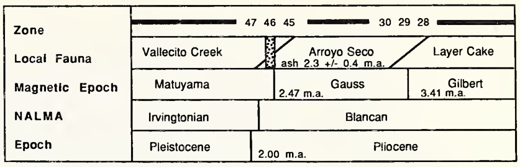

**Figure 2.** Stratigraphic markers in the fossil lizard-bearing portion of the Palm Springs Formation. Modified from Downs (pers. comm., 1986), Opdyke *et al.* (1977), and Harland *et al.* (1982).

## SYSTEMATIC PALEONTOLOGY

### Order Sauria McCartney, 1802

### Suborder Lacertilia Owen, 1842

### Infraorder Iguania Cope, 1864

### Family Iguanidae Oppel, 1811

### Subfamily Iguaninae Oppel, 1811

### *Pumilia* new genus

**DIAGNOSIS.** Referred to a group containing *Iguana* and *Pumilia* on the basis of the synapomorphic presence of a ventral quadrate process of the squamosal and fan-shaped teeth with more denticles than most other iguanines (nine or more). Differs from *Iguana* in retaining primitive conditions, including a constricted basisphenoid and teeth with fewer denticles. The strict monophyly of the type species *Pumilia novaceki** cannot be established, as all pertinent characters are primitive for both *Iguana* and *Pumilia*.

**TYPE SPECIES.** *Pumilia novaceki**.

**ETYMOLOGY.** From Latin *pumila*, meaning diminutive. Referring to the small size of this lizard, compared to its close relatives.

### *Pumilia novaceki** new metaspecies

Figure 3

**DIAGNOSIS.** The same as for genus.

**HOLOTYPE.** LACM 65116/13739.

**REFERRED SPECIMEN.** LACM 6661/78310.

**TENTATIVELY REFERRED SPECIMENS.** 6563/10600, 6661/78309, 6604/17651, 1922/10599.

**ETYMOLOGY.** In honor of my friend and colleague, Michael J. Novacek.

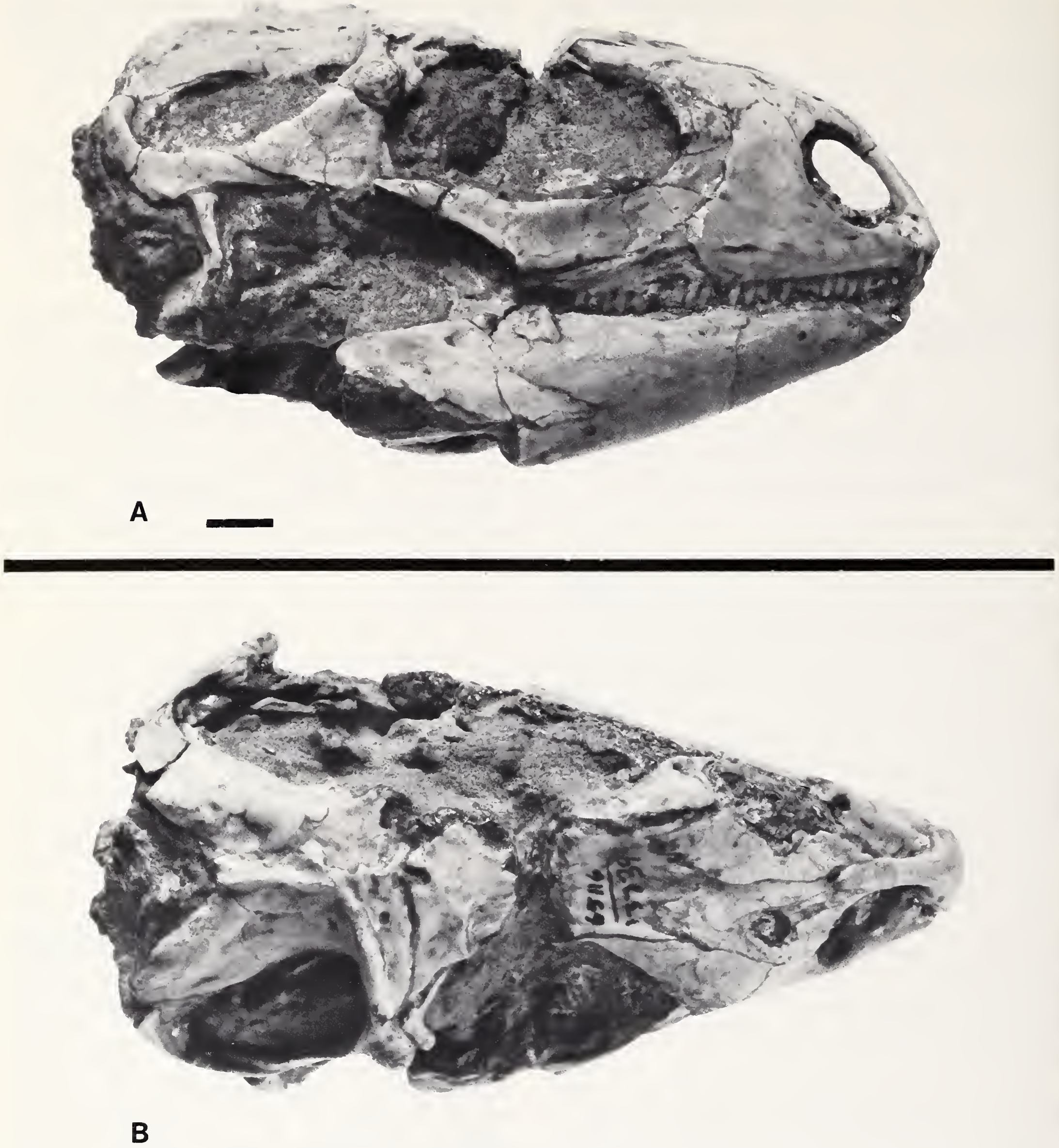

**Figure 3.** *Pumilia novaceki** n. gen. and metasp., holotype skull, LACM 13739 from LACM locality 65116. **A,** right lateral view; **B,** dorsal view. Bar = 4 mm.

DESCRIPTION OF THE HOLOTYPE. The holotype specimen (Fig. 3) is a well-preserved cranium and mandibles preserved in a fine-grained, highly indurated siltstone. The left side of the skull is crushed and laterally deformed. The braincase is separated and slightly offset from the rostrum. The dentaries and the ventral extensions of the quadrates are not preserved posteriorly. Several late ontogenetic features of *Iguana* (large prefrontal rugosity, mid-parietal ridge, and large, inflected angular process) are present. The mandibles are thick, heavy, and broken posteriorly; portions of the postdentary bones are present.

The dentary is deep and robust. Meckel's groove is closed and fused, opening anterolingually as a small slot. The Meckelian reentrant tapers anteriorly and is filled dorsally by the coronoid, medially by the large splenial, and ventrally by the angular. An anterior mylohyoid foramen lies on the triangular, slightly concave splenial. The labial surface of the dentary is smooth with four mental foramina. Posteriorly, the dentary process of the coronoid overlaps the labial surface of the dentary.

Approximately 24 teeth are present on each dentary. Most of the teeth have been damaged by airabrasive preparation or obscured by unremovable matrix and preservative. The leaf-shaped tooth crowns are compressed laterally and flare abruptly dorsal to the level of the parapet. Four small cusps, or denticles, are arranged symmetrically on each side of the apical point.

The coronoid is thick, with a posteriorly deflected coronoid process that is rounded dorsally as in young *I. iguana* Linnaeus, 1758. The angular forms the ventral surface of the mandible posterior to the dentary. Anterolabially, it and the surangular contact the dentary along a "V"-shaped suture. The labial angular–surangular contact lies along a horizontal suture.

Dorsally, the mandible posterior to the dentary is formed by the surangular. Only the smooth, convex, labial surface is visible and it is broken posteriorly. Posteriorly, the mandibles are fragmented, but the distal extension of a large, inflected angular process is present medially.

The premaxilla is undivided and forms the anterior margin of the skull. The slender nasal process forms a convex arc inserting in an incised notch in the suture dividing the paired nasals, whereas the maxillary branch forms the anterior portion of the ventral shelf in the floor of the external nares. A single ethmoidal foramen lies just ventral to each narial opening. Seven weakly serrated, almost isodont, premaxillary teeth are present.

The maxillae are large, thick, and triangular, articulating anteriorly with the maxillary branch of the premaxilla, dorsally with the nasals, and posterodorsally with the prefrontals, lacrimals, and jugals. The nares are round and deeply excavated with the anterior inferior alveolar foramina lying on posterodorsally tapering concave shelves. Six supralabial foramina and approximately 22 teeth are present. Maxillary teeth are similar to those on the dentary.

Convex nasals form the posterodorsal border of the external nares. Paired nasal rugosities are present medially. The septomaxilla is inside the narial opening and is oriented almost vertically, attaching to the roof of the nasal capsule at the nasal premaxillary suture.

The frontal forms the dorsal border of the orbit along a thick, rounded supraorbital ridge. Supraorbital foramina lie on the lateroventral surfaces. The rectangular frontal widens posteriorly and is laterally concave above the orbits. Anteriorly, it forms an incised "M"-shaped suture with the nasals; anterolaterally it articulates with the prefrontals. The frontal–parietal suture is straight and contains the parietal foramen.

The anterior and dorsal perimeter of the elliptical orbit is bounded by three bones: a ventral jugal, a medial lacrimal, and a dorsal prefrontal. The crescent-shaped jugal is dorsoventrally concave; a strut-like posterior temporal process contacts the postorbital but not the squamosal. Anteriorly, the prefrontals are thick and contact the small, angular lacrimals along horizontal sutures. At least four suborbital foramina lie on each jugal. Dorsal to the lacrimals, the prefrontals form the anterodorsal angles of the orbits and are curved, long, and taper posteriorly. A large prefrontal rugosity lies just dorsal to the lacrimal prefrontal juncture.

The triangular postorbital bounds the orbit posteriorly. The postorbital articulates anteroventrally with the temporal process of the jugal and posteriorly with the squamosal along a sinuous suture. The postorbital and jugal do not contact. Dorsally, the postorbital is constricted. Its posterior margin is concave and borders the supratemporal fenestrae. Anterodorsally, a large tuberosity is present just ventral to contact with the postfrontal. The postorbital–parietal boundary is short and lies posterior to the frontal–parietal suture.

The postfrontal is small and splinter-like, lying along the junction of the postorbital, parietal, and frontal on the inside of the orbit at the posterodorsal orbital angle.

The hourglass-shaped parietal forms the roof of the braincase. Paired anterior postorbital processes meet the postorbitals along the anterior edge of the supratemporal fenestrae. Posterior to the postorbital process the parietal is constricted. Broad, smooth, sloping surfaces form the medial boundary of the supratemporal fenestrae meeting along the midline to form a crest. Anteriorly, the crest divides and continues as ridges along the postorbital processes. Posteriorly, a deep notch is formed by the posterior extension of the supratemporal parietal processes.

The dorsally ridged, hook-shaped squamosals enclose the supratemporal fenestrae posteriorly. Squamosals do not contact the posterior processes of the jugals along the ventral postorbital margins. Posteriorly, the squamosals curve medially to connect with the supratemporals and the parietal. Ventral quadrate processes meet the tympanic crests of the quadrates. Only the triangular posterior surfaces of the supratemporals are visible, lying below the junction of the squamosals and the parietal. A narrow splinter-like process lies ventral to most of the parietal along the supratemporal fenestrae.

The quadrate is "C"-shaped with an enlarged anterolateral tympanic crest that meets the quadrate process of the squamosal and the other temporal bones at the cephalic condyle. The anterior surface of the bone is slightly convex dorsoventrally and broad and flat mediolaterally; its posterior margin is concave. Ventrally the quadrate is not preserved.

The basisphenoid and basioccipital meet in a transverse suture, defined by a small ridge just anterior to the sphenoccipital tubercles. Together these bones form the hourglass-shaped floor of the braincase. The basipterygoid processes extend anteroventrally to meet the pterygoids. The ventral surface of the basisphenoid is laterally concave, whereas the basioccipital is convex.

The pterygoid is large, with a broad, flat palatine process and a thin posteriorly oriented quadrate process. A blunt transverse process articulates with the ectopterygoid laterally. Posteriorly, the quadrate process is broken anterior to its connection with the quadrate. Pterygoid teeth are arranged on a small, ovoid pedestal anteromedial to the transverse process, not in crescentic rows as in living *Iguana* spp.; however, this condition is found in *Ctenosaura* spp. Wiegman, 1828, and some species of *Cyclura* Harlan, 1824 (de Queiroz, pers. comm.).

**DESCRIPTION OF REFERRED MATERIAL.** Only LACM 78310, a crushed skull, approximately the same size as the holotype, can be definitively assigned to *P. novaceki** due to the presence of an identical tooth morphology, a ventral squamosal process, and a constricted basisphenoid. Although the entire skull is crushed, the surangular and prearticular are well preserved. On LACM 78310, the left prearticular is connected anteroventrally with the surangular on a broad, flattened shelf. The lateral surface tapers posteriorly to the articular facet. Posteriorly, a well-developed retroarticular process with a large hook-shaped lingually inflected angular process is present. The angular and surangular lie anterior to the prearticular. Dorsally, the surangular expands and flattens posteriorly toward the articular facet. The ventrally labiolateral surface originates on the angular and continues posteriorly onto the prearticular.

**DESCRIPTION OF TENTATIVELY REFERRED MATERIAL.** The remaining material is referred to cf. *P. novaceki** on the basis of tooth morphology or a constricted basisphenoid. LACM 10600 is a dorsoventrally crushed skull of about the same size as the holotype. The skull is very incomplete in the region of critical diagnostic features; several features that undergo ontogenetic change are also not preserved. Nevertheless, the teeth are well preserved and identical to the tooth form of the holotype. Of interest are the seven conical premaxillary teeth that lack the faint serrations seen in other species of *Iguana*.

LACM 17651 and 78309 are both cranial remains of juvenile individuals. The much more complete LACM 78309 is a well-preserved, but weathered, skull that unfortunately was damaged during preparation. The skull has been laterally compressed, perhaps accentuating its high, domed appearance. The right side of the skull is better preserved than the left. The maxilla is flat and contains 15 teeth with the *P. novaceki** shape. The entire right mandible is preserved but the suture pattern is obscured. The basicranial region displays the hourglass morphology seen in the holotype.

LACM 17651 is a fragmentary specimen, represented by a posterior maxillary fragment with 12 teeth and a fragment of the jugal and ventral postorbital. The specimen is tentatively referred to *P. novaceki** because of the similarity of the teeth.

LACM 10599 is a medium-sized left dentary with a single preserved tooth. The dentary is tentatively allocated to *P. novaceki** on the basis of tooth morphology. The tooth is set in a wide dental gutter and has a long columnar shaft; the dental parapet is high and only one-half of the tooth shaft extends above the level of the parapet. The tooth crown morphology is identical to the holotype.

**DISCUSSION.** Members of the genus *Iguana* are large, neotropical members of the New World Iguanidae (Etheridge and de Queiroz, 1988). Two extant species are recognized: the widespread *I. iguana* and the Antillean *I. delicatissima* Laurenti, 1768 (Lazell, 1973). Fossils referable to the genus are known only from the Holocene deposits of Barbados (Swinton, 1937; Ray, 1964), Martinique (Hoffstetter, 1940, 1946), and the Late Pleistocene of Ecuador (Hoffstetter, 1970; Baez and Gasparini, 1977). Recent *I. iguana* reach their northern distributional limit at latitude 24°30′ in the riparian gallery forests of Sinaloa, Mexico (Hardy and McDiarmid, 1969).

The presence of a derived iguanine that forms the sister-group of species of *Iguana* in the Anza Borrego deposit is unexpected because close relatives do not live regionally. A Central American origin for the iguanines has been postulated (Etheridge, pers. comm.), based on the distribution of related forms and the relative lack of differentiation of the group in South America.

Specimens from the Palm Springs Formation are referable to the group of iguanine iguanids on the basis of fan-shaped teeth with numerous small denticles, a closed and fused Meckel's groove, and a supratemporal that lies on the medial side of the supratemporal process of the parietal (de Queiroz, 1987). Furthermore, the material is derived relative to *Cyclura* spp. in sharing with *Iguana* spp. a ventral quadrate process of the squamosal and leaf-shaped teeth with five or more small cusps (although, as pointed out by de Queiroz (1987), this last feature may be a synapomorphy of a larger group because it occurs in some other iguanines).

De Queiroz (1987) indicated that the position of the supratemporal may be a synapomorphy for iguanines. In most iguanines, including *P. novaceki**, *I. delicatissima,* and species of *Cyclura,* the supratemporal is visible from the lateral side of the skull on the supratemporal process of the parietal. In adult *I. iguana,* however, the supratemporal is usually only visible in posterior view on the inside of the occipital process of the parietal.

The shape of the basisphenoid differs among the genera of living iguanines (Etheridge, 1964a; Boulenger, 1890). Typically, the element is constricted posterior to the basipterygoid process (Fig. 4). This constriction is usually more extreme in *Cyclura* spp. (Fig. 4B, C) than in *Iguana* spp. In *I. iguana* (Fig. 4F) the basisphenoid is constricted only slightly behind the basipterygoid process. An ontogenetic shape transformation alters the proportions of the basisphenoid, yet the basisphenoid remains broad even in large individuals. Juvenile *Iguana* spp. (Fig. 4D, E) possess thin flanges forming a rectangular, ventrally concave surface. During growth, the relative length of the basisphenoid decreases, and the basipterygoid processes become thick and short, giving the basisphenoid a more constricted appearance. However, the transverse flanges remain. In *I. delicatissima,* the basisphenoid is somewhat more

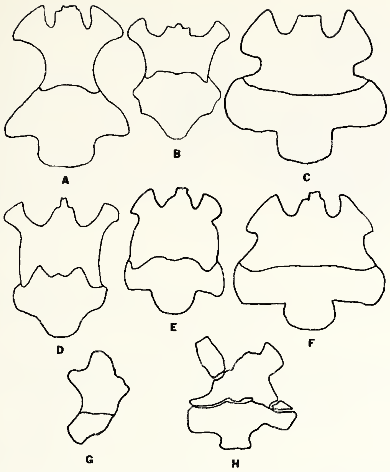

**Figure 4.** Basisphenoid-basioccipital plates of iguanines: **A**, adult *Ctenosaura pectinata* (Wiegman, 1834); **B**, juvenile *Cyclura nubila* (Gray, 1831); C, adult *Cyclura nubila*; **D**, hatchling *Iguana iguana* (Linnaeus, 1758); **E**, juvenile *Iguana iguana*; **F**, adult *Iguana iguana*; **G**, juvenile *Pumilia novaceki** n. gen. and metasp. (LACM 78309); and **H**, adult *Pumilia novaceki** (LACM 78310). Not drawn to same scale.

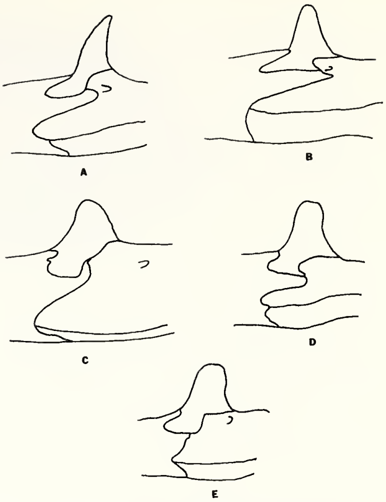

**Figure 5.** Labial view of medial mandibular elements in **A**) adult *Iguana iguana* (Linnaeus, 1758), **B**) juvenile *Iguana iguana*, C) adult *Cyclura nubila* (Gray, 1858), **D**) adult *Iguana delicatissima* Laurenti, 1768, and **E**) *Pumilia novaceki** n. gen. and metasp. (LACM 13739). Not drawn to same scale.

constricted, occasionally appearing as in some species of *Cyclura*, yet it is always wider than in *P. novaceki**. In all individuals of *Iguana* studied, the greatest constriction of the element forms a notch just posterior to the basipterygoid process.

In *P. novaceki**, the basisphenoid is constricted, lacking flanges or notches posterior to the basipterygoid process. The basipterygoid processes remain long and thin during growth as in some *Cyclura* species. In juvenile cf. *P. novaceki**, the constriction is apparent (Fig. 4A), unlike *Iguana* spp. juveniles (Fig. 4D) where the basisphenoid is wide. The condition of a constricted basisphenoid is plesiomorphic for species of *Iguana* and *P. novaceki**.

The tooth form of *Iguana* spp. changes ontogenetically. In juvenile *I. iguana*, the teeth are small with flat, broadened tooth faces and approximately eight small denticles arranged four to a side. The tooth apex is formed by a small enlarged denticle (or cusp) closely associated on either side with an additional small denticle. The teeth are widely separated and the tooth crowns are non-overlapping. In large individuals, approximately 14 denticles are present and during ontogeny the teeth become broad and fan-shaped with overlapping tooth crowns. *Iguana delicatissima* displays a similar pattern, yet large adult individuals generally have teeth with fewer denticles than in *I. iguana* of comparable size. In *P. novaceki**, the teeth are similar to the condition in *I. delicatissima*. A similar condition is also found in some members of *Cyclura* species (Lazell, pers. comm.).

In *Iguana* spp. and *P. novaceki**, a ventral process on the squamosal abuts the tympanic crest of the quadrate laterally (de Queiroz, 1987). This feature is not present in other iguanines. Although in some *Cyclura* species the squamosal may touch the tympanic crest of the quadrate, only *Iguana* spp. and *P. novaceki** have distinct processes extending ventrally to the quadrate.

In *P. novaceki** the squamosal is long and narrow and hooks medially to meet the parietal anterior to the posterior skull margin. In all species of *Iguana, Cyclura,* and *Ctenosaura* Wiegman, 1828, the squamosal is short and relatively straight, extending diagonally to meet the parietal, supratemporal, and exoccipital anterior to the posterior margin of the skull. The amount of variation in this character within species of *Iguana* and *Cyclura* prompts one to question the phylogenetic worth of this feature and makes it difficult to justify using this feature as an autapomorphy of *P. novaceki**.

The surangular of *I. iguana* has a sharp dorsal ridge. In *P. novaceki**, *I. delicatissima*, and some *Cyclura* species the surangular is more smoothly rounded posterior to the coronoid and expands posterolaterally toward the articular facet. Shapes of the coronoid and dentary also vary within *Iguana* spp. and *P. novaceki**. In *I. iguana*, the coronoid is pointed dorsally (Fig. 5A, B) and the labial surface is divided by a vertical ridge. Ventrally, a process of the coronoid extends anteriorly to the posteriormost tooth. A small posterior process extends toward the anterior surangular foramen. In *P. novaceki**, *I. delicatissima*, and *Cyclura* spp. the coronoid is dorsally rounded, smoothly concave, and not ridged. In most adult members of *Cyclura* spp. and *P. novaceki**, a posterior process of the coronoid is absent. Additionally, in *I. iguana* and some

*Cyclura* species a posterior process of the dentary extends nearly to the anterior suprangular foramen (Fig. 5). In most *Cyclura* spp., *I. delicatissima,* and *P. novaceki** only a small posterior process of the dentary exists, if at all, and it does not extend posterior to the vertical axis of the coronoid.

Derived iguanines undergo an ontogenetic skull shape transformation. During growth, the jaw becomes deeper, the cranial sculpturing more pronounced, the angular process enlarges and hooks medially, and the adductor musculature fossae on the parietal enlarge and meet at the midline of the skull forming a sagittal crest. In *P. novaceki**, many of these features occur in smaller sized individuals than in *Iguana* spp. Although the distorted fossil material tempers statistical comparisons, in both *Iguana* species only individuals with a skull length of more than 55 mm have margins of the parietal adductor fossae meeting to form distinct crests. In *I. delicatissima* this crest forms earlier (as is indicated by relative size) than in *I. iguana* (relative to total skull length), forming a very tall, thin crest that is not as long as that in adult *I. iguana.* Initially this crest forms posteriorly and extends anteriorly, reducing the size of the parietal table. In *P. novaceki**, with a skull length of 58 mm, a complete sagittal crest extending the length of the parietal is present in two individuals, a condition not reached in *I. iguana* until approximately 70 mm of skull length is attained.

A large angular process is present on the holotype and LACM 78310, a feature developed to the same degree only in large adults of extant *Iguana* spp. The shape of this process varies among species of *Cyclura, I. iguana,* and *I. delicatissima.* In *I. delicatissima, Cyclura* spp., and *P. novaceki**, the angular process is hook-shaped and thin, extending medially from a relatively short retroarticular process that narrows posterolabially. Along the labial edge of the retroarticular process lies a scar for the adductor musculature. In *I. iguana* the retroarticular process is long, thin, and straight. The angular process is wedge-shaped in juveniles and becomes more hooked in adults but retains its wedge shape relative to the primitve hooked condition.

The jugal–squamosal contact on the ventral surface of the postorbital is ontogenetically variable within genera and species of iguanines. At the level of *Iguana* spp. + *P. novaceki**, however, this character appears useful. In *I. iguana* the jugal extends along the ventral surface of the postorbital and inserts in a notch formed by the anterior opening of the squamosal–postorbital suture line. In *I. delicatissima* the jugal tapers posteriorly and does not contact the squamosal, which abuts the postorbital along a straight dorsoventral suture. In *P. novaceki** the squamosal and jugal do not contact; both the jugal and squamosal taper along the ventral surface of the postorbital. Although no ontogenetic comparisons can be made between *P. novaceki** and *I. delicatissima,* this feature does not vary in *I. iguana* with growth. In *Cyclura* spp. and in other iguanines, this character is variable, sometimes even on different sides of the same specimen.

Analysis of the characters of *P. novaceki** indicates that it is derived relative to *Cyclura* and other iguanines in having a ventral process of the squamosal. The absence of derived *Iguana* characters in *P. novaceki** easily differentiates it from species of *Iguana*; however, no characters define the strict monophyly of *P. novaceki**.

## *Dipsosaurus dorsalis* Hallowell, 1854

Figure 6

**REFERRED SPECIMENS.** LACM 6831/20930, 6559/10598, 6552/78311, 65571/10604.

**TENTATIVELY REFERRED SPECIMENS.** 6525/19693, 6715/78213, 6583/78258, 6583/78259, 6583/78560, 6583/78261, 6583/78304.

**DESCRIPTION.** The material includes small jaw fragments with three teeth as well as complete crania and mandibles. The best specimen (LACM 20930) (Fig. 6) is a skull missing only part of the rostral and temporal regions. The skull measures 25.0 mm in length, comparable in size to extant adult *Dipsosaurus dorsalis.* The premaxilla is badly worn, the nasal process is missing, and no premaxillary teeth are preserved. The right maxilla contains 15 teeth in approximately 21 tooth spaces. The teeth are uniformly tricuspid with a large, blunt median cusp flanked by smaller, blunt cusps that flare laterally, so that they slightly overlap those of each adjacent tooth; the posterior cusp always overlaps the anterior cusp of the next posterior tooth. The largest teeth are posterior to the midpoint of the tooth row. The slightly bulbous tooth crowns taper to the width of the tooth shaft before they enter the dental parapet. Faint striations occur on the enamel of some teeth.

The parietal roof, although fractured, is roughly trapezoidal and flat. The pineal foramen lies within the frontal anterior to the frontoparietal suture (Fig. 6B). A small patch of teeth is present on the pterygoid, although much of the ventral skull surface is obscured by unremovable matrix.

The right mandible is more completely preserved than the left. The thick dentary is robust; Meckel's groove is closed and fused lingually. Anterolabially, a row of four evenly spaced mental foramina are present. The coronoid is "U"-shaped with an anterior ridge that originates in a large posterior fossa.

Another specimen of note (LACM 10604) is a semiarticulated bone mass including a vertebral region and limb and skull fragments. The teeth of this specimen are identical to the three-cusped teeth in the other fossil specimens. The vertebrae represent a presacral series. Each vertebra is elongate and robust, with zygantra and zygosphenes (Fig. 7B) that are connected by a thin crest. This condition is unique to *D. dorsalis.* In other iguanines the zygantra and zygosphenes are separated by a notch (de Queiroz, 1987).

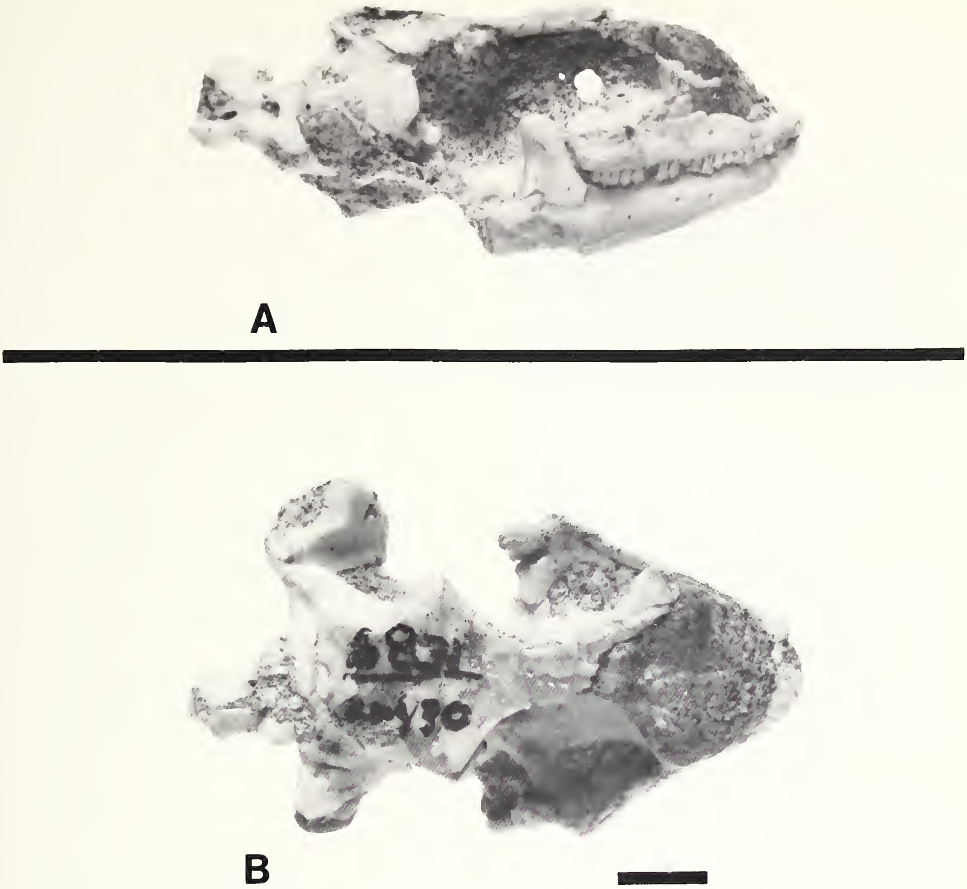

**Figure 6.** *Dipsosaurus dorsalis* Hallowell, 1852, LACM 20930, from LACM locality 6831. **A,** left lateral view; **B,** dorsal view. Bar = 5 mm.

**DESCRIPTION OF TENTATIVELY REFERRED MATERIAL.** The remaining referred material consists of bone masses that may be coprolites or owl pellets and isolated skull and dentary fragments. All of these specimens are associated with dental remains that display three- or, in one specimen, four-cusped teeth with overlapping tooth cusps.

**DISCUSSION.** *Dipsosaurus dorsalis* is a diurnal lizard of moderate size with a very high thermal optimum of 39°C (De Witt, 1967). Today *D. dorsalis* ranges throughout the southwestern United States and Sonora, Baja California, and Sinaloa, Mexico. The northern limit of this predominantly herbivorous lizard coincides almost directly with the boundary of the creosote forest community (Norris, 1953). The southern distribution of *D. dorsalis,* however, is not limited by the creosote community. In Mexico, *D. dorsalis* occurs well into arid subtropical scrub (Stebbins, 1954) habitats. *Dipsosaurus dorsalis* occupies the region of the fossil deposit today.

The only account of fossil *Dipsosaurus* is that

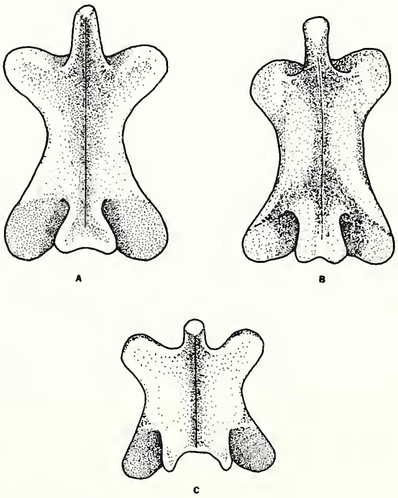

**Figure 7.** Presacral vertebrae of **A**) fossil *Dipsosaurus dorsalis* Hallowell, 1852 (LACM 10604) from LACM locality 6557; **B**) extant *Dipsosaurus dorsalis*; and **C**) *Leiocephalus melanocholorus.* Not drawn to same scale.

from the early Miocene Harrison Formation of Nebraska, originally described as *Tetralophosaurus minutus* (Olson, 1937).

De Queiroz (1987) listed eight cranial osteologic characters that are diagnostic of *D. dorsalis.* Of these, seven can be examined in the Anza Borrego fossil material, although not all on the same specimen. Only those specimens that have derived features restricted to *D. dorsalis* are positively referred to this species. The following discussion concerns characters that de Queiroz (1987) has presented as distinguishing synapomorphies of Recent *D. dorsalis.* An examination of these specimens within de Queiroz's phylogenetic framework demonstrates that only LACM 20930, 78311, 10598, and 10604 are diagnosable as *D. dorsalis.* Although other specimens show similarity to *D. dorsalis,* either the polarity of these uniting features cannot be determined, or the derived state of particular features is found in other taxa and is therefore of no use in referring these taxa to a particular species.

The presence of small, paired openings on the rostrum at the frontal nasal suture can be inferred to have been present on LACM 20930 and 78311. Although bones are not preserved in this region, impressions of these openings are present in the sandy matrix. The pineal foramen is preserved in similar fashion in LACM 10598; the cast indicates that it was entirely in the frontal. In LACM 20930 the frontal is preserved and includes the pineal foramen, the derived condition seen in Recent *D. dorsalis.*

In LACM 20930 the interior wall of the orbit indicates that the infraorbital foramen is not posteriorly bounded by a large process of the palatine. In LACM 20930 and 7831 the dorsal skull surfaces are exposed and the pterygoids "curve sharply toward midline anterior to *the* pterygoid notch" (de Queiroz, 1987), a derived condition found in most iguanines.

A single specimen (LACM 10598) preserves the retroarticular process as a mold. Recent *D. dorsalis* is unique among iguanines in displaying a retroarticular process that becomes quadrangular during ontogeny. In other iguanines, the tympanic and medial crests of the retroarticular process converge posteriorly giving adults of these species the primitive triangular-shaped retroarticular process (de Queiroz, 1987). The mold of the dorsal surface of the retroarticular process in LACM 10598 indicates that it shows the derived condition of a quadrangular retroarticular process as in large Recent *D. dorsalis.*

Dental features in the fossil specimens proved interesting. Surprisingly, only one of the fossil specimens exhibits more than three cusps on a single cheek tooth (Fig. 8B). Most extant *D. dorsalis* (Fig. 8A) have a combination of three- and four-cusped teeth, and four-cusped teeth are a synapomorphy and diagnostic character for the species (de Queiroz, 1987). Four-cusped teeth differ from the three-cusped (tricuspid) teeth in the addition of a small accessory cusp lateral to either of the flared cusps. Only LACM 78261 has four cusps on a single tooth (Fig. 8B). The four-cusped condition found in most extant *D. dorsalis* usually occurs on all of the posterior teeth. A single four-cusped tooth, surrounded by tricuspid teeth, observed in the fossil specimen was never observed in extant specimens. Four-cusped teeth are present in juveniles and adults of extant *D. dorsalis,* as well as in the purported Miocene taxon *Tetralophosaurus minutus* Olson, 1937 (=*D. dorsalis*) (Estes, 1983). Only two out of 21 Recent individuals examined possessed tricuspid teeth exclusively. Three-cusped teeth may indicate that the Anza Borrego specimens fall outside the species *D. dorsalis* as diagnosed by de Queiroz or suggest that the ancestral iguanine and basal members of this clade were polymorphic for the presence of a fourth cusp (as in *Brachylophus* Cuvier, 1829) with the fourth cusp being present in all individuals of the iguanine crown group (except *Amblyrhynchus* Bell, 1825, and some *Ctenosaura*). This possibility was suggested by de Queiroz (1987).

Generally, extant *D. dorsalis* possess seven premaxillary teeth, although fewer or more may be present (Avery and Tanner, 1971). In iguanines, seven simply pointed or tricuspid premaxillary teeth is typical (de Queiroz, 1987) although variation occurs. LACM 78311, the only specimen with a complete component of premaxillary teeth preserved, has six simple, conical teeth, a condition found in 23% of the available sample of extant *D. dorsalis* examined by de Queiroz (1987).

The Anza Borrego specimens all have pterygoid teeth. Although the loss of these has been used as a derived feature in diagnosing extant *D. dorsalis* (Etheridge and de Queiroz, 1988; de Queiroz, 1987), pterygoid teeth are occasionally present in Recent specimens. Although the Anza Borrego material differs in detail from most living *D. dorsalis,* the amount of variation present in extant populations limits the diagnostic value of the differentiating characters; hence, the Anza Borrego fossils are assigned to the living species.

Reexamination of other Tertiary lizards raises some perplexing questions, and may, on closer inspection, indicate additional fossil occurrences of *D. dorsalis.* For example, Wellstead (1982) described *Leiocephalus nebraskensis* Wellstead, 1982 (=*Leiocephalus septentrionalis* Wellstead, 1983), from the Miocene Valentine Formation of Nebraska. In discussing the relationships of *L. nebraskensis,* Wellstead states, following Estes (1963a) and Etheridge (1965, 1966), that it is "comparable only to the dentaries of *Leiocephalus* and *Liolaemus* in the common possession of a fused Meckelian groove, a scar representing the anterolabial process of the coronoid bone, and tricuspid teeth" (Wellstead, 1982:367). All of these features are found to some extent in *D. dorsalis* and the fossil material described here. Generally, the labial anterior process of the coronoid in *D. dorsalis* does not extend past the last posterior tooth. In some individuals

(Fig. 9A), the extension is identical to that seen in *L. nebraskensis* (Fig. 9B) and some extant *Leiocephalus* (Fig. 9C). The tricuspid cheek teeth of the Anza Borrego material is identical to some extant *D. dorsalis* and many *Leiocephalus* species (Pregill, 1981; pers. obs.).

Mandibular features also suggest that *L. nebraskensis* may be referable to *D. dorsalis.* In most *Leiocephalus* species, tricuspid teeth first appear posterior to the seventh dental space (Pregill, 1981), rather than in spaces two through four as in *D. dorsalis,* or four or five as in *L. etheridgei* (Pregill, 1981), *L. cuneus* (Etheridge, 1964a), or *L. nebraskensis* (Wellstead, 1982). Additionally, published figures of *L. nebraskensis* (Wellstead, 1982; pers. comm.) indicate a posterior extension of the dentary only slightly posterior to the vertical axis of the coronoid as in iguanines (Figs. 5, 9). In extant *Leiocephalus* spp. and other tropidurine iguanids examined, the posterior extension of the dentary extends well back onto the surangular, posterior to the coronoid axis (Pregill, 1981). Also in extant species of *Leiocephalus* and other tropidurines, the anterior lingual surface of the dentary below the tooth row is shallow and rounded (Robinson and Van Devender, 1973). In *D. dorsalis* and, as indicated in Wellstead's figure 1, *L. nebraskensis,* this surface is flat and deep (Wellstead, 1982:366).

Other reports of Tertiary *Leiocephalus* species from mid-continental North America also are questionable. Much of the material (Robinson and Van Devender, 1973; Setoguchi, 1978) is too incomplete for a confident identification based on diagnostic characters. Other material (Holman and Sullivan, 1981; Wellstead, 1982) referred to *Leiocephalus* spp. cannot be distinguished from some extant *D. dorsalis* and the fossil material from Anza Borrego. The single record that I consider valid evidence for a continental North American tropidurine is that from the Early Miocene Thomas Farm local fauna of Florida (Estes, 1963a). This specimen has the *Leiocephalus*-like features of small foramina in the cementum between the dentary teeth, a fused Meckelian groove, and a shallow, rounded dentary surface ventral to the tooth row. Ultimately, the definitive confirmation of North American mid-continental *Leiocephalus* species awaits better fossil material, because the genus can easily be diagnosed with skeletal material (Etheridge and de Queiroz, 1988).

## Crotaphytine group *sensu* Etheridge and de Queiroz, 1988

## *Gambelia* Baird, 1859

### Gambelia corona new species

Figure 10

**DIAGNOSIS.** Shares with other crotaphytine species the derived loss of a prefrontal, the presence of a boney labyrinth whose outlines are visible on the dorsolateral surface of the posterior braincase,

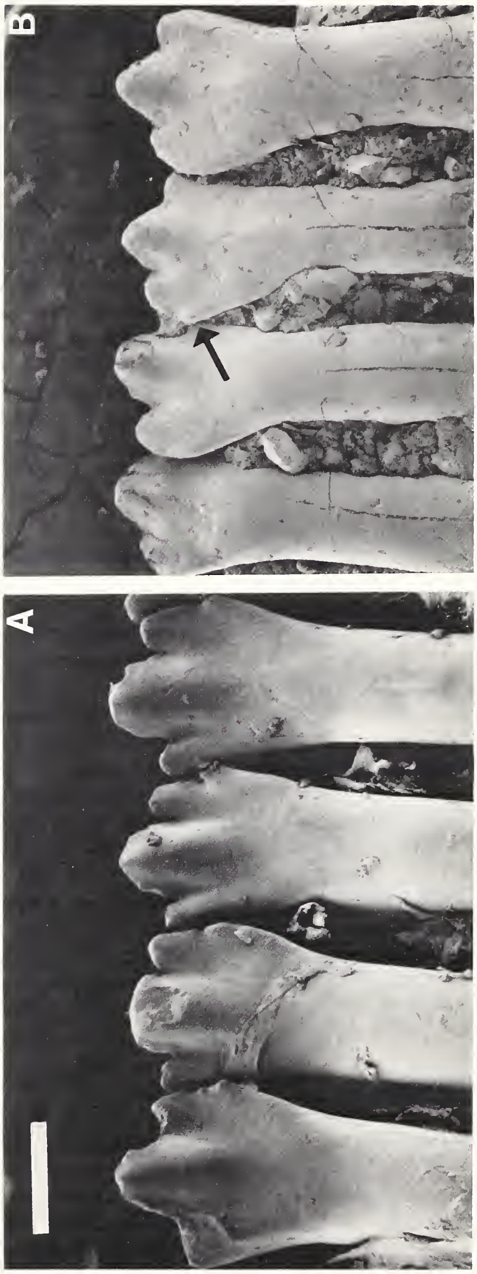

**Figure 8.** Dentary teeth of *Dipsosaurus dorsalis.* **A,** extant *Dipsosaurus dorsalis;* **B,** LACM 78261 from LACM locality 6583. Anterior toward center. Note development of accessory cusps in recent specimen and single accessory cusp in LACM 6583/78261. Bar = 0.5 mm.

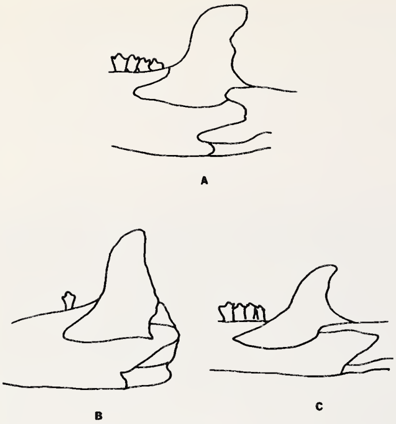

**Figure 9.** Mandibles of *Dipsosaurus dorsalis* and *Leiocephalus.* **A**, extant *Dipsosaurus dorsalis*; **B**, *Leiocephalus nebraskensis* Wellstead, 1982 (modified from Wellstead, 1982); and **C**, extant *Leiocephalus carinatus* Gray, 1852.

an elongate dentary (from Etheridge and de Queiroz, 1988), and the possession of posterior teeth with flared tooth cusps and sharp, recurved, unicuspid anterior teeth. *Gambelia corona* is a member of the genus *Gambelia* due to the shared derived presence of a Meckel's groove that is fused for more than half its length anterior to the splenial, an extremely heterodont tooth condition and a posteromedial process of the coronoid that is oriented posteroventrally. Furthermore, *Gambelia corona* has a frontal that is wider than that of other crotaphytine species and is transversally concave with supraorbital ridges, rather than flat. It can be further distinguished from other species by the unique derived presence of a frontoparietal suture anterior to the posterior extension of the orbits rather than even with the postorbital bar as in other crotaphytine species.

HOLOTYPE. LACM 7058/42880, a cranium and mandibles.

ETYMOLOGY. From Latin *corona,* meaning crown, referring to the distinguishing features of the frontal.

DESCRIPTION OF THE HOLOTYPE. Triangular in shape, the skull measures 29.2 mm in length, which is within the range of large members of extant crotaphytine species. Fused, indistinct sutures and superficial sculpturing indicate that the specimen is an adult.

The mandibles are shattered posterior to the dentary. Anteriorly, the dentary is long and thin with six mental foramina. Most of the splenial is obscured by matrix, but its anterior process fills Meckel's groove, which is closed and unfused for most of the length of Meckel's groove. Labial surfaces of the coronoids are not preserved. Lingually, the coronoid extends posteroventrally onto the surangular and angular.

The angular is shattered. On the mandible, a dorsal ridge runs between the coronoid and the articular, as in *Gambelia* spp. Ventrally, the surangular expands into a flattened surface that continues posteriorly into the articular. The angular process, although broken, appears to have been inflected. The articular condyle is broad and flat and is flanked by a medial process that rises as a protuberance on the ventral side of the mandible. Posteriorly, the articular is not preserved.

The premaxilla contains seven conical, isodont teeth. The nasal process is short and thick, as in *C. collaris* Say, 1823, and forms the anterodorsal border of the rounded external nares. The nasal process arches above the outline of the skull as in other *Gambelia* species.

The maxillae are triangular and slightly concave, although not as concave as in adult *G. wislizenii.* At least 22 teeth are present. The five posterior teeth are tricuspid, with a large median cusp and recurving tooth shafts. Anterior teeth are isodont, sharp, and recurved, extending 1.1 mm above the maxillary parapet. Five supralabial foramina are present. The ventral rim of the external nares are flattened shelves that widen anteriorly at the maxilla–premaxilla contact.

Prefrontals and nasals contact the frontal via a "W"-shaped suture. The triangular prefrontals abut the frontal along a straight suture that extends posterior to the middle of the orbits. A prefrontal knob lies on the anterodorsal angle of the orbits, and a shallow concavity lies at the median naso-frontal contact. The faintly sculptured nasals arch posteriorly. Their median contact is short, divided anteriorly by the nasal process of the premaxilla.

A laterally concave frontal forms the dorsal border of the orbits along well-developed supraorbital ridges. Posteriorly, it contacts the parietal anterior to the posterior margin of the orbits, a condition found in no other crotaphytine species examined. The parietal foramen lies on the frontoparietal suture. As in extant crotaphytine species, postfrontals are absent.

The jugal and lacrimal (the latter preserved only as fragments and matrix impressions) form the anterior and ventral margins of the orbits. The jugal is crescentic and articulates ventrally with the maxilla, sweeping posterodorsally to contact the postorbital. Several suborbital foramina and a small postorbital rugosity are present. Neither squamosal is complete; only the posterior-most contacts with the quadrate, supratemporal, and parietal are preserved. The supratemporal is narrow and wedge-shaped, lying between the squamosal, the paraoccipital process of the exoccipital, and the quadrate.

Fragments of the scleral ossicles are preserved within the right orbit.

The parietal forms the dorsal and lateral boundaries of the supratemporal fenestrae. The anterolateral processes taper to meet the postorbitals at the postorbital bars. Posteriorly, the parietal contacts the supratemporal and squamosal. Between the squamosal processes, the supraoccipital meets

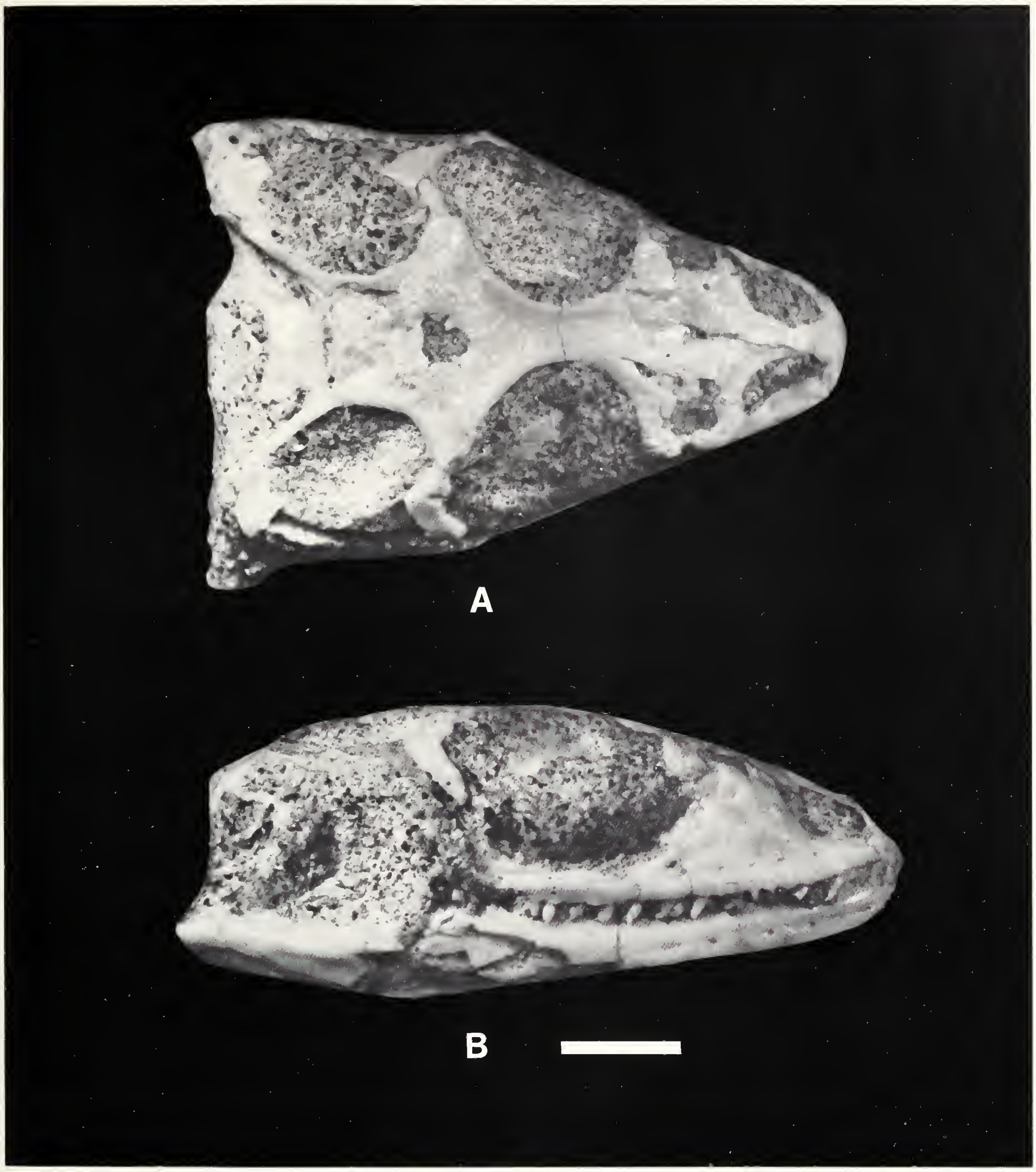

**Figure 10.** *Gambelia corona* n. sp., holotype skull, LACM 42880 from locality 7058. **A,** left lateral view; **B,** dorsal view. Bar = 5 mm.

the parietal table. The dorsal surface of the parietal is concave.

The supraoccipital has a medial, longitudinal crest and slopes gradually posterior, dorsal to the foramen magnum as in other *Gambelia* species. The outlines of the boney labyrinth of the ear are visible laterally. The paroccipital process is long and hourglass-shaped; laterally it abuts the squamosal. A shallow, medial, longitudinal groove extends approximately half the length of the process, just lateral to the braincase.

The quadrate is "C"-shaped. Dorsally it contacts the paroccipital process, the supratemporal, and the squamosal. On the posterior quadrate surface, a large concavity, bordered by the tympanic crest, tapers toward the ventral condyle.

The basioccipital and basisphenoid are fused into an hourglass-shaped unit. Paired sphenoccipital tubercles are present laterally; anteriorly a pair of thick basipterygoid processes reach anteroventrally to the pterygoids. Between the basipterygoid processes lies a parasphenoid process.

The pterygoids are largely concealed by unremovable matrix, yet a single row of small pterygoid teeth are present on a longitudinally extending ridge along the medial pterygoid boundary. Posteriorly this ridge flattens as the pterygoid narrows anterior to articulation with the ectopterygoid.

Anterior to the pterygoids lie the palatines, which display small palatine teeth in a shallow depression.

**DISCUSSION.** Crotaphytine species are well known from western North American Pleistocene deposits (Etheridge, 1958; Holman, 1970; and others). Most of the material has been referred to *C. collaris.* Fossil occurrences of *G. wislizenii* (Baird and Girard, 1852) are restricted to the Holocene in the southwestern deserts (Van Devender and Mead, 1978; Van Devender and Worthington, 1978; Brattstrom, 1958; Norell, 1986). Holman (1972) described the Early Oligocene *C. oligocenicus,* from Saskatchewan, Canada, on the basis of fragmentary material. This species has several very primitive iguanid features, and its reference to *Crotaphytus* is questionable (Estes, 1983). The presence of Pliocene *G. corona* in California marks the earliest undisputable occurrence of the genus and of the group.

Within the crotaphytines, two diagnosable generic groups have been recognized (Weiner and Smith, 1965; Etheridge and de Queiroz, 1988), although this suggestion has been somewhat controversial (Montanucci *et al.,* 1975; Montanucci, 1969). The genus *Crotaphytus* contains three species: *C. collaris, C. reticulatus* Baird, 1858, and *C. insularis* Van Denburgh and Slevin, 1922, and the genus *Gambelia* contains only *G. wislizenii* and *G. silus* (Stejneger, 1893). Many workers consider *G. silus* a subspecies of *G. wislizenii.* Etheridge and de Queiroz (1988) provided a diagnosis for the group and the two genera. Although the characters that these authors present in support of the monophyly of these groups cannot all be considered exclusively apomorphic at this level (due to a lack of resolution of outgroup taxa), they state that "the unity of the crotaphytine group is not controversial" and that "Both *Crotaphytus* and *Gambelia* possess derived characters supporting their separate monophyly" (Etheridge and de Queiroz, 1988:322).

Whereas *G. corona* differs from all other crotaphytine species in diagnostic characters, it shares several features with other *Gambelia* species. The nasal branch of the premaxilla in *Crotaphytus* spp. conforms to the outline of the rostrum. In species of *Gambelia* (including *G. corona*) the nasal process arches, protruding dorsally in lateral view from the skull outline. The external nares of *G. wislizenii* are more ovoid and elongate than those of either *G. corona, G. silus,* or *C. collaris,* and this may be a synapomorphy of the species. However, comparative material for *G. silus* was very limited.

In species of *Crotaphytus,* the dorsal surface of the surangular is expanded and flat, with the opening to the suprangular foramen directed almost vertically in a shallow depression between two faint longitudinal ridges. Posteriorly, a prearticular process hooks lingually anterior to the articular condyle. In *Gambelia* species the dorsal surface of the surangular is ridge-like with no dorsally flattened surface, and there is a labially directed anterior surangular foramen. Also in *Gambelia,* a narrow shelf of bone connects the entire lingual prearticular process with the surangular, forming a posterolingual shelf that expands posteriorly to the articular condyle making the prearticular process less distinct than in species of *Crotaphytus.* In species of *Gambelia* the ventral extension of the coronoid on the inside of the jaw onto the angular and surangular occurs in a posterior arc, whereas in *Crotaphytus* spp. the extension is almost vertical.

Much discussion has centered on the dental morphology of crotaphytine species. Weiner and Smith (1965) indicated that the condition found in *G. wislizenii* (including *G. silus*) is heterodont, with anterior haplodont, median diconodont, and posterior triconodont (their terminology) teeth grading into each other. *Crotaphytus collaris* exhibits a subheterodont condition. Robinson and Tanner (1962) noted that the teeth of *G. wislizenii* are narrower and longer than the broad, short teeth found in the '*collaris*' group. Montanucci (1969) disputed these conclusions by pointing out that these categories are subjective, influenced by ontogeny, and contain intergradational forms. Nevertheless, while intermediates between the heterodont and subheterodont conditions are found, the sharp, recurved anterior teeth found in most *G. wislizenii* are never developed to the same degree in species of *Crotaphytus.* Only the maxillary teeth (the dentary teeth are hidden by unpreparable matrix) of *G. corona* are sufficiently free of matrix to allow inspection. *Gambelia corona* has 22 teeth, compared with 17 to 22 teeth in *G. wislizenii* and 14 to 20 in *Crotaphytus* species (Weiner and Smith, 1965). The size, cusp pattern, and recurved aspect of the fang-like anterior teeth and triconodont posterior teeth in *G. corona* approximate the condition seen in *G. wislizenii* and *G. silus,* and like the arched premaxillary process, is suggestive of a sister-group relationship.

The frontal of *G. corona* is wider than any other crotaphytine species observed and has a pair of supraorbital ridges along the dorsal border of the orbits, giving the frontal a laterally concave aspect. Some adult *C. collaris* display slightly concave frontals; the supraorbital ridges, however, are never as well defined as in *G. corona.* Some other iguanids acquire concave frontals late in ontogeny, and some also show supraorbital ridges. This feature may simply be a coincidence of large size and a wide frontal, but because it is not seen in other crotaphytine species, it is considered here to be derived.

The repositioning of the frontoparietal suture is perhaps correlatd with a widening of the frontal. In other iguanids, the frontoparietal suture lies behind the posterior angle of the orbits, abutting the postorbital bar. In *G. corona* the frontoparietal suture lies along the posterodorsal border of the orbit, anterior to the postorbital bar.

The basisphenoid in *C. collaris* articulates with the basioccipital in a long, straight transverse suture. In *G. wislizenii,* branches of the basisphenoid extend posteriorly to the sphenoccipital tubercles of the basisphenoid. This condition also occurs in sceloporines, iguanines, and morunasaurines. *Gambelia corona* displays the condition seen in *C. collaris.*

My decision to retain the name *Gambelia* for this species may seem to be a violation of the principles for naming taxa described in the methods section. Here my intention is to not cause a proliferation of names. Because I cannot demonstrate that the two recent *Gambelia* species form a monophyletic group independent of *G. corona,* it seems pointless to assign this species to a new genus at this time. In the event that *G. corona* is found to be the sister-group to these species it should be placed in a new, as yet unnamed, genus.

## Sceloporine group *sensu* Etheridge and de Queiroz, 1988

## *Phrynosoma* Wiegmann, 1828

### ***Phrynosoma anzaense* new species**

Figure 11

**HOLOTYPE.** LACM 6822/64595.

**DIAGNOSIS.** Shares with all other *Phrynosoma* species parietal and squamosal cranial horns. Shares with *P. mcalli* the derived presence of a supratemporal fenestra that is constricted by flanges from the surrounding bones. Differs from all other *Phrynosoma* by possessing accessory horns ventral to the largest squamosal horn.

**ETYMOLOGY.** In reference to the type locality in the Anza Borrego desert.

**DESCRIPTION OF THE HOLOTYPE.** LACM 64595 is a posterior skull region in a poorly indurated sandstone nodule (Fig. 11). The parietal, left squamosal, and left postorbital are the only complete dorsal skull elements. The left jugal, frontal above the orbit, prefrontal, and right postorbital are present but broken. The basioccipital and basisphenoid are the only basicranial elements present.

The prefrontal is roughly triangular. The anteromedial surface is not broken, but detached from the nasal and frontal along the suture joint. Laterally, an extensive supraorbital process sweeps posteriorly forming the dorsal rim of the orbit. In some *Phrynosoma* species this process meets the supraorbital process of the frontal forming a supraciliary rim. Because the prefrontal has been rotated diagonally, this association cannot be examined in LACM 64595; the supraorbital process is large, however, compared to most other *Phrynosoma* species examined. Anterior to the supraorbital process the orbital rim plunges ventrally to an assumed, but missing, contact with the maxilla. Sculpture, in the form of small rugose protuberances, is present along the dorsal orbital rim.

The frontal is incomplete. Anterior to the frontoparietal suture the frontal is broken into right and left components. The frontoparietal suture extends from the posterior angle of the orbits through the pineal foramen. Although broken, a thick supraorbital process extends forward on top of the diagonally rotated supraorbital process of the prefrontal. The frontal margin along the supratemporal fenestra is covered with rough tubercles. A large horn lies at the posterolateral border of the bone above the posterior angle of the orbits. The broad, flat area between the orbits is covered with rugose tubercles.

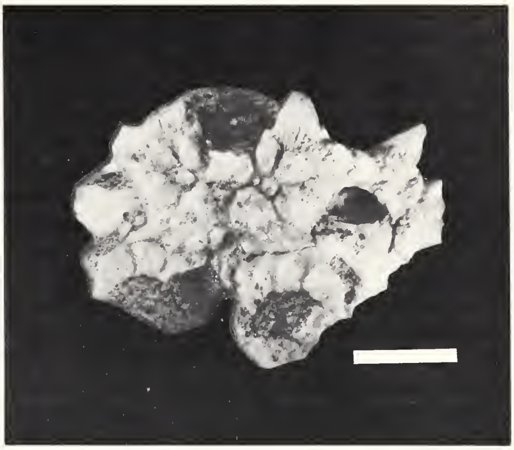

**Figure 11.** Cranium of *Phrynosoma anzaense* n. sp., LACM 64595 from LACM locality 65116. Bar = 5 mm.

The hourglass-shaped postorbital abuts the frontal and parietal dorsally, and the jugal and squamosal ventrally. The arched anterior surface forms the posterior margin of the skull. The nearly vertical posterior surface borders the anterior limit of the semicircular supratemporal fenestrae. The surface of the postorbital is sculptured with small granular tubercles.

The fragmentary jugal forms part of the ventral orbital margin. Two small horns occupy the laterally oriented face of the bone. One lies in the wide area directly below the postorbital bar. Anterior to the posterior angle of the orbit, a second, better defined horn lies near the orbital rim. Just ventral to these horns the jugal is broken.

The heavily sculptured squamosal forms the posterolateral border of the skull. Along the lateral squamosal border, three unequally sized horns point posterolaterally. The two anterior horns are broken distally but have joined bases. Judging from relative base size, the anteriormost horn appears to have been smaller than the median or posterior horn. The jugal–squamosal suture lies just anterior to the base of the anterior squamosal horn. The posterior horn is largest and is separated from the anterior pair of horns by a short diastema. The apex of the posterior horn projects posteriorly; its dorsal and ventral surface is sculptured and striated. The squamosal and parietal form the posterior margin of the cranium. Medial to the posterior squamosal horn lies the suture where the squamosal abuts the parietal. The thin, flat interior surface of the squamosal forms half of the curved posterior border of the supratemporal fenestrae. The dorsal squamosal surface is covered by large tubercles. Dorsal and ventral large single tubercles lie both between the single posterior and paired anterior horns and at the postorbital, jugal squamosal suture. Although the ventral surface of the squamosal is poorly preserved it apparently lacks sculpture.

The parietal forms the dorsal roof and posterior margin of the specimen. It is a large, rugose, roughly triangular bone with a pair of horns emanating from its posterolateral border. These horns are broken just distal to their bases. Larger than the squamosal horns, these parietal horns are also sculptured and have striations running along their axes. Between the horns a small spine on a tubercle projects posteriorly. The pineal foramen is a "U"-shaped notch in the parietal at the frontoparietal suture. The parietal margin of the supratemporal fenestra is formed of very thin bone. The parietal bar contacts the squamosal lateral to the large parietal horns and a small accessory horn that is located on a large tubercle on the lateral base of the main horn. Two other tubercles ring the base of each parietal horn. The entire dorsal surface of the parietal is heavily sculptured, with a prominent group of four tubercles in a transverse "V"-shaped row just posterior to the pineal foramen.

The only basicranial elements preserved are the basisphenoid and basioccipital. The latter is compressed longitudinally with a large occipital condyle posteriorly and a pair of smooth sphenoccipital tubercles laterally. The suture between the basioccipital and basisphenoid lies anterior to the sphenoccipital tubercles. The basisphenoid is transversally concave and tapers from posterior to anterior. Two basipterygoid processes extend anteriorly from the anterior margin of the basisphenoid.

**DISCUSSION.** The most recent review of extant *Phrynosoma* recognizes 14 species (Montanucci, 1987). Estes (1983) listed an additional three fossil species from the Neogene of western North America. Montanucci's review allows *P. anzaense* to be evaluated within a comparative framework.

Several features of the jugal were considered to be phylogenetically informative by Montanucci and therefore may aid in determining the phylogenetic affinities of *P. anzaense.* The posterior border of the jugal in *P. anzaense* is expanded posteriorly, and the jugal surface is covered with tuberosities. Montanucci considered this condition derived for a group composed of the species *P. modestum* Girard, 1852, *P. platyrhinos* Girard, 1852, *P. mcalli* (Hallowell, 1852), *P. solare* (Gray, 1845), *P. cornutum* Harlan, 1825, *P. coronatum* Gray, 1857, *P. orbiculare* (Linnaeus, 1651), and *P. douglassi* Girard, 1858. Furthermore, *P. anzaense* shares with all of these taxa, except *P. douglassi* and *P. orbiculare,* a jugal with an anteriorly sloping posterior border and a jugal surface with tuberosities. Apparently, Montanucci considered that the processes were a continued transformation of jugal rugosities, although this is not made explicit. *Phrynosoma anzaense* shares with *P. solare, P. mcalli, P. platyrhinos,* and *P. modestum* an enlarged scale at the base of the parietal horn.

Except for *P. mcalli* and *P. anzaense,* all horned lizards have relatively large, ovoid supratemporal fenestrae. In no case is the width of the posttemporal bar nearly as wide as the anteroposterior width of the supratemporal fenestrae in *P. anzaense* and *P. mcalli.* In the latter, outgrowths from the parietal, frontal, and postorbital bones almost, or sometimes completely, cover the supratemporal opening, a feature responsible for its original placement in the monotypic genus *Anota* (Hallowell, 1852). Only in *P. anzaense* and *P. mcalli* do flanges of bone extend into the supratemporal fenestrae from the entire circumference of the fenestrae, resulting in a construction of the opening. The condition found in *P. anzaense* is not as well developed as in any *P. mcalli* examined. In addition, no *P. mcalli* examined showed the degree of development of cranial sculpture found in *P. anzaense.* My initial analysis (Norell, 1983) of the *P. anzaense* condition as less constricted than *P. mcalli* was questioned by Montanucci (1987), who suggested that this may simply represent the condition found in early ontogenetic stages of *P. mcalli.* However, because the type specimen of *P. anzaense* represents a mature individual (as can be determined by the degree of cranial sculpture, the extensive development of cranial horns and the degree of fusion of the cranial sutures), I doubt that this is the case.

Because the pattern of squamosal horns is used in the diagnosis of *P. anzaense,* the distribution of this feature among *Phrynosoma* species is discussed. This feature was not used by Montanucci as a phylogenetic character. However, due to the extensive phylogenetic variation seen in this feature it may be of phylogenetic and diagnostic value. The relative size and number of squamosal horns varies among species of *Phrynosoma. Phrynosoma asio* Cope, 1864, possesses two large posteriorly directed horns on each squamosal. Two or three squamosal horns are present in *P. coronatum* and *P. douglassi* Girard. In *P. asio* the bases of the horns are separate. At the anterior base of the anterior squamosal horn, a very small accessory horn is variably present along the squamosal jugal suture. In juvenile *P. coronatum,* horns with separate bases are present. During ontogeny, the horn bases join. In large individuals a pair of small rugose accessory horns are present; one of these small pointed horns lies dorsal and posterior to the base of the posterior squamosal horn, and the other dorsal to the junction of the large horn bases. *Phrynosoma cerroense* (Stejneger, 1893) and *P. taurus* Duges, 1864, apparently also have two squamosal horns (Presch, 1969) and *P. ditmarsi* Stejneger, 1907, possesses four squamosal horns. Specimens of these species were unavailable for study.

Most species of horned lizards display a pattern of three sagittally aligned squamosal horns, and in all cases the anterior horn is smaller than the two posterior horns. In *P. mcalli* and *P. cornutum,* the two posterior squamosal horns are large and approximately equal in size, but in *P. platyrhinos* the horns increase in dimension posteriorly. *Phrynosoma orbiculare* has an anterior small squamosal horn, a short median horn expanded at its base, and a long posterior horn with a constricted base. All squamosal horns are evenly spaced in *P. platyrhinos, P. orbiculare,* and *P. mcalli.* In *P. cornutum* and *P. douglassi,* the anterior two horns are joined at their bases. Dorsal accessory horns, like those in *P. coronatum,* are present in *P. mcalli, P. cornutum,* and *P. orbiculare.* Horned lizards with three squamosal horns that were not available for this study were *P. boucardii* and *P. braconieri* (Presch, 1969).

The diminutive *P. modestum* and the large *P. solare* both possess four squamosal horns. In *P. solare* these horns are large, joined at the bases, and increase in size posteriorly. In *P. modestum* the two anterior horns are large, although not as large as the posterior horn and joined at their bases. The third posterior horn is very small, lying in between the bases of the second and fourth posterior horns. Identification of this horn may be the reason for the discrepancy between my observation of four horns and Montanucci's (1987) observation of three. Neither *P. solare* nor *P. modestum* possess small ventral accessory horns. The unstudied *P. ditmarsi* is reported to have three squamosal horns (Montanucci, 1987).

*Phrynosoma anzaense* has three large horns on its squamosal, a common pattern in other *Phrynosoma* species. The anterior horns of *P. anzaense* are fused at the base with the anteriormost horn having the relatively smaller base. The third horn is short and broad, although not as short as in *P. orbiculare* or *P. douglassi. Phrynosoma anzaense* is the only horned lizard examined that has an accessory horn ventral to and between the second and the third horns.

Considerable confusion surrounds the number of horns on the posterior parietal margin among *Phrynosoma* species. In all species of *Phrynosoma,* the posterior border of the parietal is elaborately sculptured with large horns. It can safely be determined that the pattern of two large posterodorsally directed horns is the modal condition; however, in *P. solare, P. modestum,* and large *P. douglassi* four parietal horns may be present. But only in *P. solare* is the additional pair of horns significantly developed. A single small median horn that lies between the large horns is present in some species. This horn originates on a bony "osteoderm" along the parietal border and is large in *P. coronatum, P. cornutum,* and *P. orbiculare.* This condition may appear as a small oblique horn in some *P. mcalli* and *P. platyrhinos* and is present in the type specimen of *P. anzaense.*

A dense pattern of "osteoderms" covers the entire parietal table. These "osteoderms" are not the true osteoderms formed by intermembraneous bone found in some other lizards (*e.g.* helodermatids, anguides, and varanids), but simply the bony origin of the cranial scalation (Etheridge, pers. comm.). For want of a better term "osteoderm" is used here. The extremely rugose surface of *P. anzaense* is formed of these "osteoderms." Montanucci, although not polarizing these conditions, indicated that "low tuberosities, and conical spine-like tubercles represent progressively derived conditions" (Montanucci, 1987:8). At the base of the large parietal horn in *P. anzaense* lies a single row of sharply pointed "osteoderms," one of which is large and protruding. This feature is a synapomorphy for a group including *P. modestum, P. mcalli,* and *P. platyrhinos* (Montanucci, 1987).

The shape of the parietal and its association with the postorbital and squamosal determine the shape of the supratemporal fenestrae. In *P. anzaense* the suture between the parietal and squamosal lies near the middle of the arching posttemporal bar. Owing to the position of the squamosal–parietal suture, a distinct sculptured squamosal process of the parietal is present. In *P. asio, P. cornutum,* and *P. solare* this suture lies at the lateral base of the parietal horn, not lateral to an accessory horn as in *P. anzaense.*

The distribution of derived character states used by Montanucci (1987) in analyzing the phylogeny of *Phrynosoma* species indicates that *P. anzaense* is the sister-group to *P. mcalli* in a group containing these species and *P. platyrhinos, P. solare,* and *P. modestum.* Several alternative phylogenies are equally parsimonious for this clade, although Montanucci preferred the topology of a sister-group relationship between *P. platyrhinos* and *P. modestum* with *P. mcalli* and *P. solare* as sequential sister-groups.

Species of the genus *Phrynosoma* are poorly known from the early and middle Neogene of North America, only becoming common in Late Pleistocene cave deposits. The earliest occurrence of a *Phrynosoma* species is in the Late Miocene Valentine Formation of Nebraska (Estes and Tihen, 1964). This dentary lacking sculpture or horns is not referred to a species. By the Late Pleistocene specimens referable to extant taxa are present (Brattstrom, 1953, 1955; Etheridge, 1960; Holman, 1970). Three fossil species have been described from Pliocene and Pleistocene beds: *P. adinognathus* (Rickart, 1976) from the early Pleistocene of Kansas, known only from a pair of dentaries and allied with *P. douglassi* (Van Devender and Eshelman, 1980); *P. holmani* (Eshelman, 1975) from the Late Pliocene of Kansas, originally described as a *Sceloporus*; and *P. josecitenses* (Brattstrom, 1955) from the Pleistocene of Nuevo Leon, Mexico, consisting of a skull fragment with four temporal spines and of unknown affinities. All fossil remains are found within the western United States and northern Mexican range of the genus.

Recent *Phrynosoma* species occupy a wide range of habitats, from the mesic yellow-pine forest to desert grassland species *P. douglassi* to the xeric *P. platyrhinos,* making any paleoecologic comparison tenuous. Recent *Phrynosoma* species are diurnal and insectivorous; fecal material and stomach contents show a diet that is almost entirely of ants (Stebbins, 1954). *Phrynosoma mcalli* and *P. platyrhinos* occur as extant species at or near the fossil locality.

## *Phrynosoma* sp.

**REFERRED SPECIMEN.** LACM 6604/78293, a badly weathered cranium.

**DESCRIPTION.** Anteriorly both maxillae and prefrontal and nasal fragments are preserved. Portions of the jugal and postorbital delineate an oval orbit. Part of the right squamosal is the only temporal element present. The bone is severely weathered and pitted.

**DISCUSSION.** The specimen is referred to *Phrynosoma* species indeterminate on the basis of the distinctive peg-like dentition. The very fragmentary nature of the material (such as the lack of a temporal region) preclude lower level comparisons. The only character of note is that LACM 78293 shares with *P. modestum, P. mcalli, P. platyrhinos,* and *P. solare, P. taurus, P. cornutum,* and *P. braconnieri* the derived character of a prefrontal that borders the external nares separating the maxilla and the nasals.

## Sceloporine Type A

Figure 12D

**REFERRED SPECIMENS.** LACM 6583/78235, 6540/78305, 6540/78306, 6540/78307, 1454/(unnumbered specimen), 1196/78211, 1196/78212, 6712/20981, 1615/4401, 1615/78721, 1615/78276, 1615/78272, 1113/123323, 1114/78205, 1114/123320, 1114/123321, 1114/123322, 1114/123334, 1114/123333, 6707/78241, 1297/64126; dentary and maxillae fragments.

**DESCRIPTION.** Sceloporine Type A is a large sceloporine with low-crowned teeth and long columnar tooth shafts. The tooth crowns are tricuspid with a central median cusp and oblique lateral cusps. The central median cusp is bulbous, its outline continuing onto the tooth shaft.

The best specimen, LACM 123320 (Fig. 12D), is a left mid-dentary fragment with eight teeth in 15 tooth spaces. Meckel's groove is closed, but unfused anterior to the Meckelian reentrant. Anteriorly, Meckel's groove flares open. The labial surface of the dentary is smooth with two mental foramina. The teeth are low crowned, reaching less than one-fourth their height above the dental parapet.

The tooth shafts are long, columnar, and curved with resorption pits present at the bases of teeth three, five, and seven; nutrient foramina occupy the remaining tooth bases. The tooth crowns are tricuspid, however, most of the teeth are worn, giving them an oblique appearance. The central bulbous cusp is flanked by small lateral cusps. The tooth crowns are lingually concave and have striated enamel. The anterior teeth are smaller than those posterior in the jaw.

The remaining materials are fragments of dentaries and maxillae referred to sceloporine Type A on the basis of a similar dental morphology of low-crowned teeth with long columnar shafts and weakly developed tricuspid teeth. A large size range is represented by this material, yet all sizes display similar dental morphology except that the smaller dentaries have teeth with higher crowns, extending approximately one half their height apical to the parapet.

**DISCUSSION.** Living sceloporines (*sensu* Etheridge and de Queiroz, 1988) form a monophyletic group comprising ten genera and 105 species. Sceloporines can be divided into four generic groups: a *Petrosaurus* Boulenger, 1885, group, a *Urosaurus* Hallowell, 1854–*Sceloporus* Wiegman, 1828–*Sator* Dickerson, 1919–*Uta* Baird and Girard, 1852, group (the sceloporus group of Etheridge and de Queiroz), a *Phrynosoma* group, and a sand lizard group containing *Callisaurus* Blainville, 1835, *Uma* Baird, 1859, *Cophosaurus* Troschel, 1850, and *Holbrookia.* Most of these taxa inhabit south western North America. Etheridge (1964b) described the generic morphologies of the sceloporines and proposed a phylogeny for this informal grouping that has been improved by Etheridge and de Queiroz's (1988) cladistic treatment of these groups' relationships.

In sceloporine Type A, the teeth are low crowned with small lateral cusps. In extant sceloporines, the tooth form within most genera is regular. The most aberrant pattern is seen in *Callisaurus,* which have pointed, blade-like, and unicuspid teeth. Other sand lizards show a more typical iguanid pattern of high-crowned tricuspid teeth. In species of *Holbrookia* and *Cophosaurus* the tooth columns are cone-shaped with expanded bases and small lateral cusps that may be separated from the median cusp by shallow "V"s if the teeth are unworn. In *Uma* spp., the teeth are also very high crowned, have expanded bases, and are more tricuspid than in other sand lizards with lateral cusps widely separated from the median cusp.

The two species of *Petrosaurus* form the sister-group of other sceloporines (Etheridge, 1964b). The teeth are tricuspid with wide laterally expanded crowns and flaring cusps in *P. thalissinus* (Cope, 1863), or tall, slender, and widely spaced, with less flaring cusps in *P. mearnsi* Van Denburgh, 1895. Both species have widened tooth bases. The members of the *Phrynosoma* group are highly distinctive in their small, occasionally tricuspid, cylindrical peg-like teeth.

The *Uta–Urosaurus–Sator–Sceloporus* group has a variable tooth morphology. In *Uta* sp., the teeth are high crowned with expanded cylindrical bases.

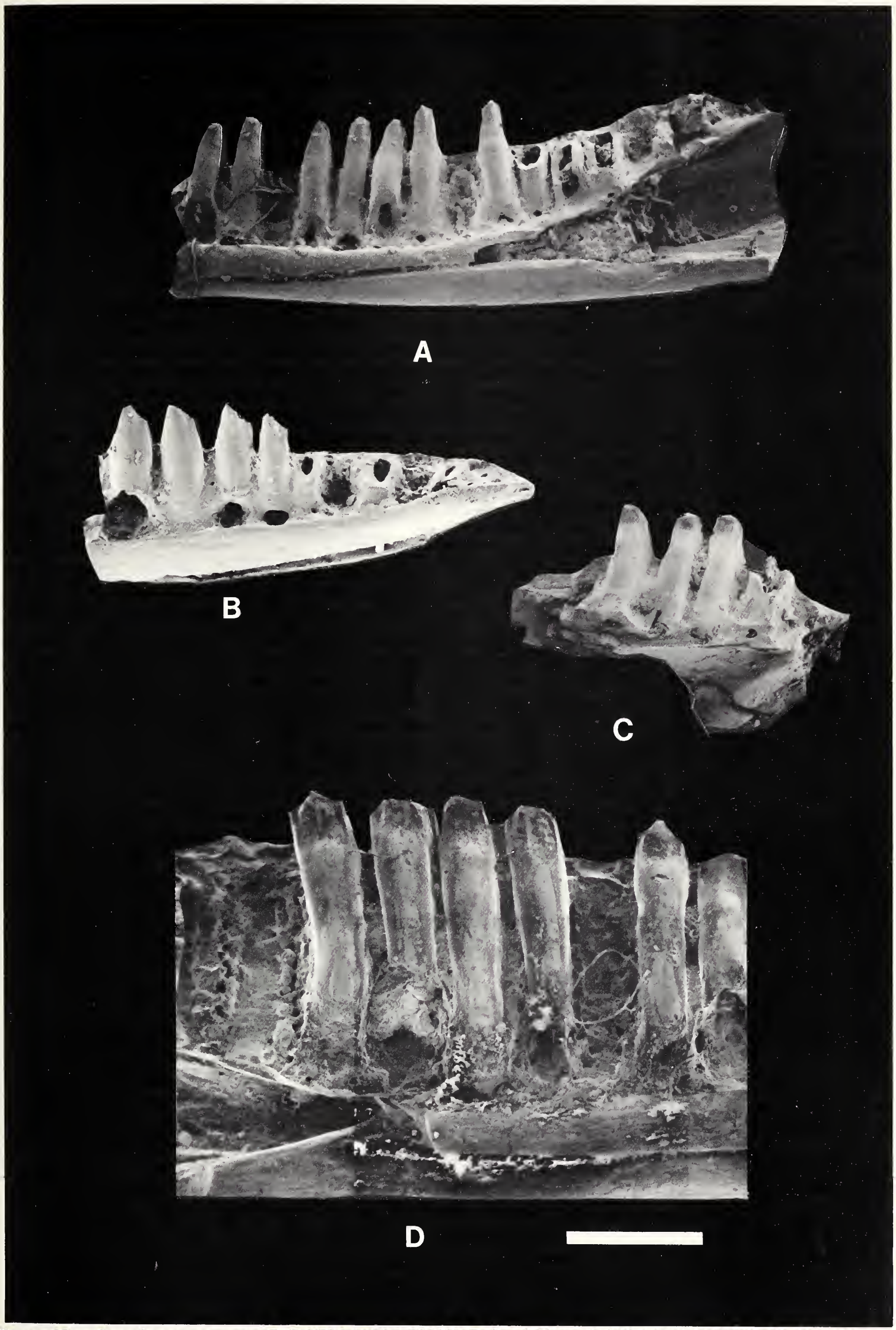

Figure 12. **A,** sceloporine species B (LACM 1114/123330); **B,** basal Teiini (LACM 1114/123326); **C,** *Eumeces* sp. (LACM 1615/78308); and **D,** sceloporine species A (LACM 1113/123323). Bar = 1 mm.

The unerupted teeth are tricuspid with a large, central median cusp. In worn teeth, the ventral cusp is blunt and the lateral cusps form small shoulders unseparated from the central cusp. *Urosaurus* spp. are small *Uta*-sized lizards with dental morphology that is indistinguishable from some small *Sceloporus* species or *Uta* sp.

*Sator* sp. has strongly tricuspid teeth with columnar bases. The tooth crowns are laterally compressed. The lateral cusps are separated from the main cusp by shallow "V"s that continue onto the crown surface.

The genus *Sceloporus* is large (70 species) and morphologically diverse (Smith, 1939). Typical *Sceloporus* species have low-crowned, columnar, tricuspid teeth, although much variation is seen in this pattern. In many large *Sceloporus* species, as well as sceloporine Type A, the tooth crowns are curved, giving them a dorsally concave appearance. This modification, as well as crown height, is enhanced during ontogeny with overall deepening of the dentary.

The assignment of these specimens to any taxon within the sceloporine group (except for those taxa that can be eliminated) cannot be defended until a better understanding of the hierarchic distribution of sceloporine characters is achieved. Even with such information, the level of morphologic resolution of such material may never allow such determinations. For instance, Wellstead (1982) and Larsen and Tanner (1974) found no consistent means of distinguishing taxa on the basis of jaw morphology. The Anza Borrego specimens are considered as identifiable morphotypes within the sceloporine group until more detailed information is developed.

## Sceloporine Type B

Figure 12A

**REFERRED SPECIMENS.** LACM 6583/78246, 6583/78247, 6583/78248, 6583/78249, 6583/78250, 1615/4401, 1114/123330, 1114/123331, 1114/123332; fragmentary dentaries; unnumbered specimens possibly referable to sceloporine Type B are found at localities 1461, 6683, 1454.

**DISCUSSION.** Several small *Uta*-sized dentaries with delicate, very high-crowned teeth are designated sceloporine Type B. The better specimens (Fig. 12A) exhibit teeth that extend over half of their height above the dental parapet. The teeth are cone-shaped, tapering toward small tricuspid, laterally compressed crowns. The median tooth cusps are relatively large, bulbous, and pointed. The lateral cusps are small, flat, and separated from the median cusps by small "V"s that extend onto the tooth columns. The expanded tooth bases and tapering tooth columns give the teeth a widely spaced appearance at the crowns. The tooth bases are excavated by small nutrient foramina or resorption pits.

Meckel's groove is unfused and closes anterior to the extension of the splenial. The lingual surface of the jaw is rounded and the teeth are set in a shallow dental gutter that expands anteriorly.

The labial surface of the jaw is smooth with small mental foramina anteriorly. Posteriorly, a broad fossa is present dorsally and tapers anteriorly on the large better preserved specimens. Overall the dentary is straight, long, and thin.

**DISCUSSION.** Sceloporine Type B resembles *Uta* sp. in its small size, teeth with wide bases tapering distally, and high-crowned weakly tricuspid teeth. Unfortunately, other small sceloporines also display a similar pattern, and reference of sceloporine Type B to a lower level taxon cannot be justified.

## Infraorder Scincomorpha Camp, 1923

## Superfamily Lacertoidea Oppel, 1811

## Family Teiidae Gray, 1827

## Tribe Teiini Gray, 1827

## *Ameiva* Meyer, 1795, and/or *Cnemidophorus* sp. Wagler, 1830

Figure 13

**REFERRED SPECIMENS.** LACM 6831/20929, a nearly complete cranium and mandibles.

**DESCRIPTION.** The rugose cranial osteoderms and the heavily sculptured mandibles indicate that the individual was an adult. Anteriorly, the rostrum is crushed and the premaxilla, nasals, most of the prefrontals, and the anterior parts of the maxillae and dentaries are missing. Posteriorly the postorbital bars, squamosals, left quadrate, most of the jugals, and the retroarticular process of the dentaries are not preserved.

**DISCUSSION.** Within the family Teiidae, Vanzolini and Valencia (1965) recognize two tribes. The tribe Teiini contains the genera *Ameiva, Cnemidophorus, Teius* Merrem, 1820, *Dicrodon* Duméril and Bibron, 1839, and *Kentropyx* Spix, 1825. A second tribe, the Tupinambini, contains the genera *Dracaena* Daudin, 1802, *Crocodilurus* Spix, 1825, *Tupinambis* Daudin, 1802, and *Callopistes* Gravenhorst, 1838. Presch (1974) indicated that within the Teiini, only the genera *Teius, Dicrodon,* and *Kentropyx* are monophyletic and that *Dicrodon* shares derived features with *Teius.* Species of *Kentropyx* possess a single derived feature, a concave parietal, but species of *Ameiva* and *Cnemidophorus* do not share any derived features not common to all Teiini. Presch (1970) reported that species of *Ameiva* possess a tongue sheath, although this feature may vary within the genus (Burt, 1931; Vanzolini and Valencia, 1965). Rieppel (1980) reported that differences exist in the temporal musculature between *Ameiva* spp. and other members of the Teiini, but his sample was limited to two species of *Ameiva* and a single species of *Cnemidophorus.*

Species of *Ameiva* and *Cnemidophorus* are morphologically indistinguishable, and these genera are of dubious monophyly. Estes (1963a) suggested that the genera *Ameiva* and *Cnemidophorus* be synonymized under the name *Ameiva* to eliminate confusion. However, because the genus *Ameiva* is still undiagnosable as a monophyletic taxon, this suggestion is not accepted here until further work demonstrates the monophyletic elements of the *Ameiva/Cnemidophorus* species complex.

LACM 20929 is comparable with extant species of the *Ameiva/Cnemidophorus* complex in its weakly bicuspate teeth and slightly convex parietal. During growth *Ameiva/Cnemidophorus* species undergo a great deal of ontogenetic change (Estes and Williams, 1984), osteoderms are fused onto the skull roof and extensive dermal sculpture occurs on the mandibles, with the dentary becoming thick, robust, and sculptured, and the teeth losing their blade-like appearance, becoming short and peg-like. These features in the fossil specimen suggest that it was senescent, a stage unrepresented in the sample of comparative material. Until additional comparative material representing corresponding ontogenetic stages becomes available for study, referral of this specimen in any species-level taxon is unsupported. Nevertheless, the fossil does possess some interesting features. The overhang of the parietal into the supratemporal space, forming a small roof, is more developed in the fossil than in any species of extant *Ameiva/Cnemidophorus* studied. In these specimens, the adductor muscles generally attach on the dorsal surface of the parietal. In *Kentropyx* species this condition is more extreme, and the parietal roof extends far into the supratemporal space. In some older individuals of *Ameiva/Cnemidophorus* spp., rudiments of this condition become apparent.

Living Teiini occur predominantly in South America. The genera *Teius, Dicrodon,* and *Kentropyx* are confined to the Neotropics. *Ameiva* species (exclusive of *Cnemidophorus*) exist in South America, the Caribbean, and north into Mexico, whereas species of *Cnemidophorus* live in North America southward into southern South America. Two species (*C. tigris* Baird and Girard, 1852, and *C. hyperythrus* Cope, 1863) occur in the area of the fossil deposit today. Species displaying *Ameiva/Cnemidophorus* dental morphologies are common elements of Neogene North American assemblages. However, these specimens may have been overinterpreted (Estes, 1983; Norell, 1986), and the referral of this material to species should be reinterpreted.

## Tribe Teiini Gray, 1827

### Genus and species indeterminate

Figure 12B

**REFERRED SPECIMENS.** LACM 6583/78300, 1454/123325, 1615/78299, 1114/123326, 1114/123327, 1114/123328, 1114/123329, 1114/78194; fragmentary maxillary and dentary fragments.

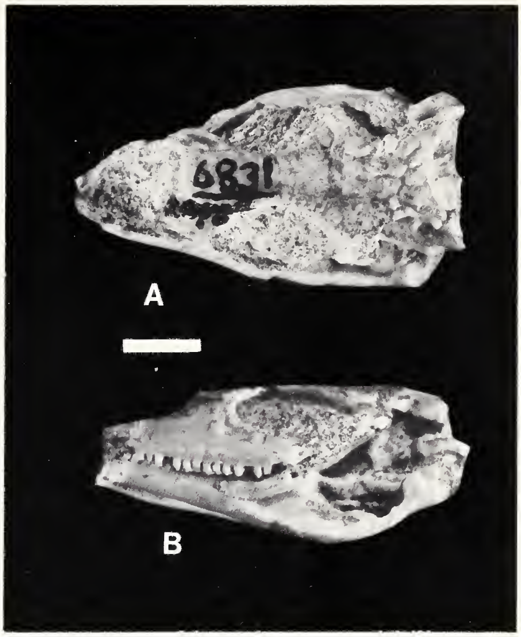

**Figure 13.** Skull of *Ameiva/Cnemidophorus* LACM 20929 from LACM locality 6831. **A,** dorsal view; **B,** left lateral view. Bar = 6 mm.

**DISCUSSION.** This material is referred to the tribe Teiini on the basis of tooth morphology. These teeth are blade-like and either two- or three-cusped. This tooth morphology is undoubtedly primitive for the Teiidae (Presch, 1974) and is present in *Kentropyx, Ameiva,* and *Cnemidophorus.*

## Superfamily Scincoidea Oppel, 1811

## Family Scincidae Oppel, 1811

## Subfamily Scincinae Oppel, 1811

## *Eumeces* Wiegmann, 1834

### *Eumeces* sp.

Figure 12C

**REFERRED SPECIMENS.** LACM 6522/123324, 1437/78277, 1437/178236, 1615/78308; fragmentary dentaries and maxillae.

**DESCRIPTION.** The most nearly complete specimen, LACM 78308 (Fig. 12C), is a small (2.2 mm) maxillary fragment containing four teeth. The labial surface of the maxilla is smooth and contains four supralabial foramina, two of which are incomplete. Lingually, five tooth positions are present on a dental shelf. The teeth are low crowned, only projecting 0.37 mm above the maxillary parapet. The tooth columns curve labially from crown to base. Small nutrient foramina are present at the expanded base of each tooth. The tooth crowns are of approximately equal height and width. The striated, lingually concave crowns are canted transversally. The three anterior teeth are worn and separated by equal interdental spaces. The apex of the posterior tooth is relatively more pointed, perhaps indicating that it was newly erupted.

**DISCUSSION.** Species of *Eumeces* form a primitive, inadequately diagnosed, probably paraphyletic genus of the subfamily Scincinae (Estes, 1983; Greer, 1970). Extant species are found in North America, southwestern Asia, northern Africa, China, and Japan (Greer, 1970). All of the fossil material is confined to North America, with the exception of a Middle Miocene species from Morocco (Rage, 1976). The earliest occurrence of the genus comes from the Early Miocene Thomas Farm locality of Florida (Estes, 1963a).

Specimens are referred to the genus *Eumeces* on comparable tooth morphology and interdental spacing (Estes, 1963a). *Eumeces* species have unicuspid, slightly bulbous, pleurodont teeth, with lingually concave surfaces below obtuse apices. Small ridges on the lingual tooth surfaces form the blunt apices. The concave lingual surface of each tooth is covered by fine enamel striations that terminate abruptly at the base of the crown.

Aside from the problems of referring the fossils to *Eumeces,* the fragmentary nature of the material makes specific assignment difficult. *Eumeces skiltonianus* Baird and Girard, 1852, most closely resembles the fossil specimens in general dental similarity. Two skinks occupy the immediate and surrounding area today: *E. gilberti* Van Denburgh, 1896, and *E. skiltonianus. Eumeces gilberti* is a large species, and adults are easily distinguished from the fossil material by their low crowned bulbous teeth with blunt apices. Relative size, general morphologic similarity, and geographic affinity are, however, not sufficient criteria to allow specific identification.

## Superfamily Cordyloidea Fitzinger, 1826

## Family Xantusiidae Baird, 1858

## *Xantusia* Baird, 1858

### ***Xantusia downsi** new metaspecies**

Figure 14

**DIAGNOSIS.** A small xantusiid (tooth row length = 2.87 mm), referred to the genus *Xantusia* (*sensu* Savage, 1963) on the basis of the synapomorphic reduction of tricuspid teeth and a smaller size. *Xantusia downsi** can be distinguished from other species of *Xantusia* by the plesiomorphic presence of a dental gutter. All distinguishing characters of the type species *Xantusia downsi** are plesiomorphic for the genus *Xantusia.*

**HOLOTYPE.** LACM 1114/123301, a right spleniodentary.

**REFERRED SPECIMENS.** LACM 1114/78198, 1114/123302, 1114/123303, 1114/123304, 1114/123305, 1114/123306, 1114/123307, 1114/123308, 1114/123309, 1114/123310, 1114/123311, 1114/123312, 1114/123313, 1114/123315, 1114/123316, 1114/123317, 1114/123318, 1114/123319, 1114/123335, 1323/78292, 6583/78244, 1615/78274; spleniodentary, maxillae, and frontal fragments.

**ETYMOLOGY.** Named in honor of Theodore Downs for his contribution to our knowledge of Anza Borrego paleontology.

**DESCRIPTION OF THE HOLOTYPE.** Meckel's groove is closed and fused, opening anteriorly at the mandibular symphysis. A large coronoid process curves posterodorsally and is broken above the level of the tooth crowns. A weak coronoid incision lies lingual to the surface of the coronoid process. Posterolabially, the spleniodentary is broken. A coronoid notch reaches the posteroventral edge of the subdental shelf and borders the anterior mylohyoid and inferior alveolar foramina. A deep subdental gutter forms the dorsal surface of a heavy ventral ridge. Thirteen tooth positions are closely spaced. The first, second, and fifth teeth are missing. The teeth are of equal height and rise approximately one-half of their height above the dental parapet, above which the tooth columns taper to bluntly conical, laterally compressed apices. The tooth enamel is smooth, and the anterior teeth are slightly more pointed and blade-like than the posterior ones. Teeth seven and twelve are excavated at their bases by resorption pits while the bases of the remaining teeth contain nutrient foramina. The labial surface of the dentary is robust and convex. Mental foramina are present below the fifth, seventh, tenth, and twelfth teeth. Posterolabially a smooth, saddle-like fossa lies ventral to the dorsal ridge between the coronoid process and the last tooth.

**DESCRIPTION OF REFERRED SPECIMENS.** The referred material indicates that several characters found on the holotype specimen are variable within the taxon. The dental gutter is not as well developed in some of the specimens; nevertheless, it is always more developed than in any *Xantusia* spp. examined. The specimens with a small dental gutter are smaller and not as robust as the holotype specimen.

The splenial depression seen in some species of "*Paleoxantusia*" Hecht, 1956 (Schatzinger, 1980) occurs variably in *X. downsi**. This depression demarks the boundary of the splenial (Gauthier, pers. comm.). A few specimens (LACM 123319 and 123307) have depressions in the region of the inferior alveolar and anterior mylohyoid foramina, whereas similar sized specimens lack this feature.

Maxillae are referred to *X. downsi** on the basis of dental morphology, size, and occurrence at the same locality (LACM 1114). All of the maxillae are fragmentary; the best specimen (LACM 123316) contains nine conical teeth, identical to those in the holotype spleniodentary.

Four frontals from LACM locality 1114 have been provisionally assigned to *X. downsi** because they are xantusiid-like and occur in the same lo-

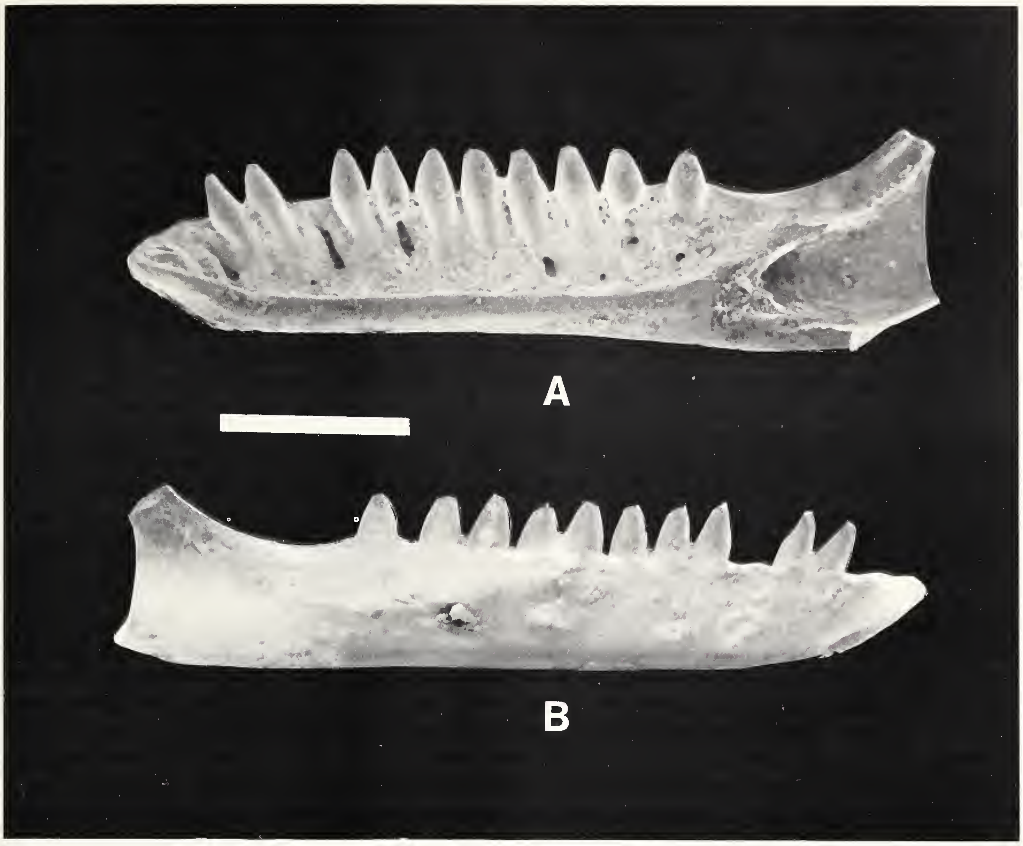

**Figure 14.** Holotype spleniodentary of *Xantusia downsi** n. metasp., LACM 123301 from LACM locality 1114. **A,** lingual view of left spleniodentary; **B,** labial view of left spleniodentary. Bar = 1 mm.

cality with the type dentary material. The frontals resemble *X. vigilis* Baird, 1859, in size and shape, being small and paired with an anterior descending process; however, they are slightly larger than in *X. vigilis.*

**DISCUSSION.** Living xantusiids constitute three (Bezy and Sites, 1987) or four (Crother *et al.,* 1986) monophyletic generic groups; another group, the fossil genus "*Paleoxantusia,*" is "paraphyletic as presently constituted" (Estes, 1983:125).

Contemporary phylogenetic treatments of xantusiids are difficult to apply to the Anza Borrego fossil material because few characters are preserved in these specimens. Here, *Xantusia downsi** is placed as the probable sister-taxon of *Xantusia* on the basis of reduction of the tricuspid teeth, small size, and more delicate dentary compared with members of the "*Paleoxantusia*" grade and other xantusiids.

The tooth form of living species of *Xantusia sensu* Savage (1963) and Crother *et al.* (1986) (including only *X. vigilis* and *X. henshawi*) is usually conical with blunt posterior teeth grading into sharper anterior teeth. In some individuals, minute lateral cusps are present on teeth near the middle of the tooth row. The teeth are often slightly laterally compressed and show a slight lingual concavity. Small enamel striations are present near the bases of the tooth crowns. The condition in *X. downsi** is similar, except that the teeth are more robust and begin to taper toward the apices at the level of the dentary parapet rather than dorsally and lack striations on the tooth crown bases.

*Xantusia downsi** is not referable to species of the extant taxa *Lepidophyma* Duméril, 1851, *Cricosaura typica* Gundlach and Peters, 1863, or *Klauberina riversiana* (Cope, 1883) on the basis of dental morphology and tooth number. In *K. riversiana* the teeth are trifid, with flaring lateral cusps placed in a single line (Hecht, 1956; *contra* Crother *et al.,* 1986). *Lepidophyma* species have posterior teeth with a unique pattern of lateral cusps rotated lingually, forming a superficially tribosphenic molar-like crown. The teeth of *Cricosaura typica* are low crowned with blunt apices. Species of "*Paleoxantusia*" show highly variable tooth patterns. In *P. borealis* Holman, 1972, the teeth have minute lateral cusps. "*Paleoxantusia*" *fera* Hecht, 1956, and *P. allisoni* Schatzinger, 1980, show diminutive lateral cusps while in *P. kyrentos* Schatzinger, 1980, the teeth are distinctly trifid but without flaring lateral cusps and the posterior teeth are somewhat molariform.

A smooth groove on the labial surface of the coronoid process for insertion of the adductor musculature is present in some xantusiids and is variably present in *X. downsi**. The holotype exhibits a smooth coronoid process, however, LACM 123305 as well as other specimens have smooth, furrow-like grooves, just ventral to the dorsal edge of the coronoid process, that extend posteriorly. Specimens with this condition are smaller and more delicate than those with a smooth coronoid process.

No extant *Xantusia* species studied displays the distinct subdental gutter seen in *X. downsi**. This feature, which occurs in some "*Paleoxantusia*" and other xantusiids, is primitive for the genus *Xantusia.* The dentary is also more robust and deeper in *X. downsi** than in *X. vigilis* or *X. henshawi. Xantusia henshawi* has a long, thin dentary quite distinct from all other xantusiids. The dentaries of *X. vigilis* and *X. downsi** are short, however, the dentary of *X. downsi** is more heavily constructed and more like "*Paleoxantusia*" (especially "*P.*" *fera*) than *X. vigilis.* Measurements taken of the labial dentary depth at the penultimate posterior tooth on *X. vigilis* gave a mean depth of 0.69 mm (20 specimens measured) compared to 0.79 mm for *X. downsi**. These values are statistically different.

Although there is some overlap in the morphologies of *X. downsi** and *X. vigilis,* almost all of the Anza Borrego specimens are readily distinguished from other *Xantusia* species. The most recent phylogenetic treatment of the Xantusiidae failed to support a single phylogenetic hypothesis on morphologic grounds (Crother *et al.,* 1986). One hypothesis was, however, congruent with an hypothesis based on chromosomal information (Bezy, 1972) that suggested a sister-group relationship between *K. riversiana* and species of *Xantusia.* However, further work by Bezy and Sites (1987) on allozyme data indicated that *Klauberina* may be derived from within *Xantusia.*

The two extant species of *Xantusia* are diagnosable and may form a monophyletic group exclusive of other Xantusiidae (Crother *et al.,* 1986). Provisionally, I consider *X. downsi** to be their sister-group, lacking the derived features of a thin, lightly constructed jaw, and the loss of the dental gutter. *Xantusia downsi** is designated a metataxon because no diagnostic unequivocally derived features were discovered. It is tempting to consider *X. downsi** as representative of a new genus that is the sister-taxon to *Xantusia.* However, because the monophyly of *Xantusia* has been questioned by Bezy and Sites (1987) this suggestion is dependent on further phylogenetic analysis of this group.

Xantusiids are poorly known in Neogene deposits, however, unstudied *Xantusia*-like forms are present in the Late Miocene age Ricardo Formation, the Middle Miocene Barstow Formation (Gauthier, pers. comm.), as well as at Late Pleistocene localities along the Mojave River, San Bernardino County, California. Whistler (1984) reported on an additional Early Middle Miocene specimen of possible "*Paleoxantusia*" grade from the Boron Local Fauna of southern California. This specimen is, however, unreferrable to *Xantusia* on the basis of derived characters. Pleistocene specimens referred to the genus *Xantusia* (Brattstrom, 1953) from Rancho La Brea are apparently iguanids (Estes, 1983).

Living species of *Xantusia* are small, secretive, nocturnal or crepuscular lizards that are either saxicolous or live under decomposing yucca and agave. Both *X. vigilis* and *X. henshawi* inhabit the general region of the Anza Borrego deposit today.

## Infraorder Anguinomorpha Furbringer, 1900

## Superfamily Anguioidea Gray, 1825

## Family Anguidae Gray, 1825

## Subfamily Gerrhonotinae Tihen, 1949

## Genus and species undetermined

Figure 15

**REFERRED SPECIMENS.** LACM 6552/10601; cranium and mandibles.

**DESCRIPTION.** The skull is laterally deformed and weathered on the right anterolateral side; most of the right side of the basicranium and the temporal regions are fragmentary. Overpreparation prior to my study of the specimen fragmented most of the cranial osteoderms and destroyed all teeth in the left maxilla.

**DISCUSSION.** The specimen is referable to the anguid subgroup Gerrhonotinae on the basis of the presence of an anterior process of the surangular, a fused surangular, prearticular, and articular, long anterior and posterior maxillary processes, and the presence of the derived conditions of a fused frontal that is constricted above the orbits, long thin supratemporals and frontoparietal scales in contact on the midline (Estes, 1983; as modified from Meszoely, 1970, Gauthier, 1982, and Good, 1987).

A specific or generic assignment of the Anza Borrego gerrhonotine is difficult to defend with character information. Until recently, no comparative treatment of the osteology of the extant gerrhonotines has been undertaken. Good's (1987, 1988) review of gerrhonotine osteology and phylogeny is difficult to apply to the Anza Borrego specimen, because most of the features considered in this work are not preserved or difficult to interpret in the Anza Borrego fossil. Furthermore, the gerrhonotine group is speciose and poorly represented in osteologic collections, disallowing detailed comparison of species at this time.

Of the 96 characters Good (1987) used in establishing relationships within the Gerrhonotinae, only a few can be directly examined. The following discussion is based on Good's work and polarities of characters were extracted from his analysis.

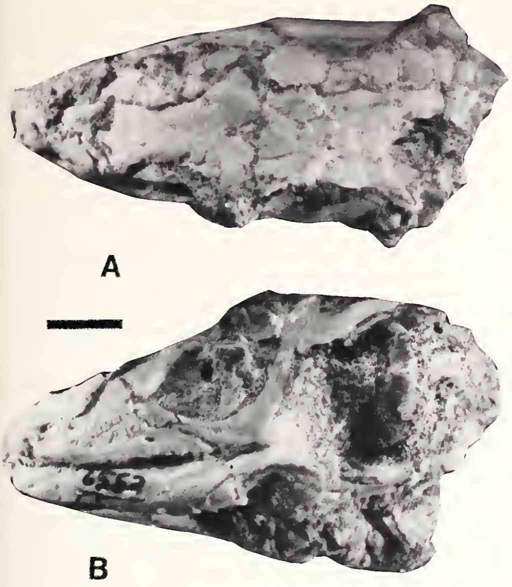

**Figure 15.** Unidentified fossil gerrhonotine, LACM 10601 from LACM locality 65116. **A**, dorsal view; **B**, left lateral view. Bar = 4 mm.

The specimen displays a number of features primitive for the entire gerrhonotine group, including a narrow premaxillary process, a maxilla that does not extend markedly posterior to the ultimate tooth, an unexpanded cephalic condyle of the quadrate, a lacrimal furrow lying at the lacrimal–prefrontal suture, an elongate surangular, a parietal that is visible in lateral view (although this may be an artifact of crushing), and a labial dentary surface lacking a subdental groove.

Derived characters that can be observed on this specimen are few and difficult to interpret. Nevertheless these characters may indicate relationship with a subgroup of gerrhonotines. The Anza Borrego specimen shares with all gerrhonotines, except *Gerrhonotus* Wiegman, 1828, species, a maxilla–prefrontal suture that is not straight; whether the condition in the fossil specimen is like that in species of *Abronia* Gray, 1838 (a "W"-shaped suture), cannot be determined. The fossil specimen also shares a label expansion of the posterior dorsal surangular with this group.

A few features suggest a special relationship with species of *Abronia*. These features include the shared derived presence of a supralabial groove on the maxilla dorsal to the posterior teeth and the reduction of the lateral concave surface of the quadrate. In addition to these characters, the fossil specimen exhibits the derived presence of a lacrimal and jugal everted at the maxillary suture. Relationship with *Abronia* is contradicted by the lack of a posterior groove on the dentary ventral to the tooth row, a derived feature found in species of *Abronia* and its immediate sister-groups but lacking in LACM 10601.

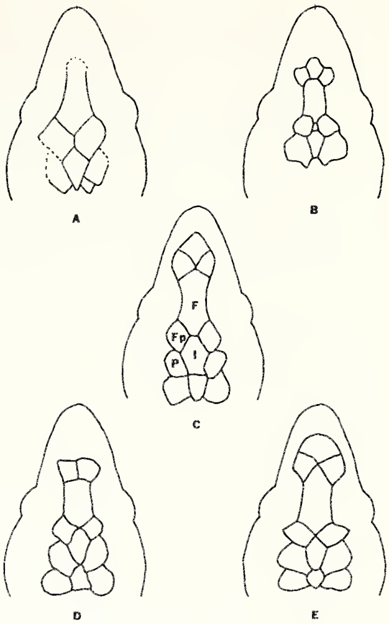

**Figure 16.** Cranial osteoderms of gerrhonotines. **A**, LACM 10601, **B**, *Abronia ornelasi* (modified from Campbell, 1984), **C**, *Gerrhonotus liocephalus infernalis*, **D**, *Barisia imbricata*, and **E**, *Elgaria coerulea*. (C–E modified from Waddick and Smith, 1974). F, frontoparietal; Pa, parietal; Fp, frontoparietal; Ip, interparietal.

Assessing the relationships of this specimen within the phylogenetic system proposed by Good is difficult, because so few features are well enough preserved to allow detailed comparison. Similar difficulties lead Good (1988) to remove all but two of 166 previously referred specimens from the gerrhonotinae. Although LACM 10601 is well preserved, by fossil standards, its relationships are still unclear.

In addition to the cranial characteristics listed above, the pattern of cephalic osteoderms found in the Anza Borrego specimen is unique among gerrhonotines examined during this study. *Abronia taeniata* (Wiegmann, 1834) has large, heavily sculptured cranial osteoderms, unlike the fine sculpturing seen on other gerrhonotines, except for the moderately sculptured *Barisia imbricata* (Wiegmann, 1834)/*gadovi* (Boulenger, 1913) group and the fossil *P. ricardoensis*. Unique to *P. ricardoensis* is a pattern of osteoscutes on the frontal in which a single anterior osteoscute is bordered posteriorly by a relatively high number of irregularly shaped osteoscutes (Estes, 1963b), a pattern present in LACM 10601. The frontal scute pattern of the Anza Borrego specimen is unusual in the broad contact between the frontoparietal scutes at the midline. The characteristic gerrhonotine frontal pattern appears to be a single, large anterior frontal scute and a pair of frontoparietal scutes partially separated by the anterior portion of the interparietal scute (Fig. 16). In *A. taeniata* the frontoparietal scutes are narrowly separated by a posterior projection of the frontal scute. The Anza Borrego specimen has two frontoparietal scutes in contact along the midline anterior to the terminus of the interparietal scute. However, this morphology may be subject to variation (Estes, pers. comm.), limiting is phylogenetic efficacy.

Gerrhonotines form a natural group of morphologically and behaviorally diverse forms. *Abronia* spp. are specialized arboreal and generalized forms, while *Elgaria* Gray, 1838, and *Gerrhonotus* are composed of generalized species with large ranges. The species *Elgaria multicarinata* Fitch, 1934, occupies the general region of the locality today. Although fossils from as far back as the Late Cretaceous (Armstrong-Ziegler, 1978) have been referred to the Gerrhonotinae, Good (1988) indicates that these determinations were premature. The earliest occurring taxon that shares apomorphy with a gerrhonotine subclade is *Paragerrhonotus ricardoensis.* This specimen is a member of the gerrhonotine crown group and, therefore, is part of the Gerrhonotinae *sensu stricto,* even to the point that Good (1988) noted this taxon should perhaps be synonymized with *Abronia.* It is interesting that this additional regional occurrence of a fossil gerrhonotine shows affinities with the gerrhonotine crown group; Recent members of this clade are native to central Mexico. The putative presence of these related taxa in the Late Tertiary of southern California suggests that the distribution of this group was once more widespread.

## PALEOECOLOGY

The climate of the Anza Borrego region changed dramatically during the period of time represented by the Palm Springs Formation. During the Neogene, North American climate had deteriorated from warm subtropical and tropical in the Late Miocene and Early Pliocene to cold and arid in the Late Pleistocene (Hibbard, 1960). Deposition of the Palm Springs Formation occurred during the Early and Late Pliocene and Early Pleistocene epochs, correlative with the Blancan and Early Irvingtonian land mammal ages.

Evidence from a deep-well core at Searles Lake, California (Liddicoat *et al.,* 1980) suggests that the Nebraskan glacial stage, occurring near the middle of the Vallecito Creek local faunal zone, signified the onset of more mesic or pluvial conditions in the region, approximately 1.8 ma. Although the area of the deposit was never glaciated, regional glacial conditions near Mammoth Lakes (Inyo County, California), signified by the Deadman Pass Glacial Till (Currey, 1966), may indicate a general cooling trend in local conditions beginning 3.1 ma.

Following the onset of the initial Nebraskan continental glaciation, glacial activity culminated, receding at the beginning of the Aftonian interglacial, which corresponded with the top of the Palm Springs Formation. The effect of the large scale glaciation in periglacial areas has been debated. Conditions during glacial maxima are thought to have been more mesic than during periods of glacial retreat (Auffenberg and Milstead, 1969). Experimental modeling evidence contradicts this reasoning, as wet conditions are correlated with general glacial retreat and aridity with glacial advance (West, 1977). The close proximity of large Sierra Nevadan ice sheets may have brought runoff into the Colorado River drainage. The Palm Springs Formation is intercalated with oyster beds (Downs and Woodard, 1961), and tectonic evidence caused Johnson *et al.* (1983) to suggest that deposition of the entire section occurred at or near sea level.

Lizard producing localities from Anza Borrego extend through 2500 m of section representing approximately two million years of deposition. Considering the probable climatic change during the Late Pliocene and Early Pleistocene in the Anza Borrego desert and the large scale temporal mammalian faunal replacements (Downs and White, 1968), changes in lizard community composition would not be surprising.

Figure 17 indicates the stratigraphic occurrence of lizard fossils in the Palm Springs Formation. Taxonomic composition of the assemblage changes temporally. Most obvious is the disappearance of the iguanine genera *D. dorsalis* and *P. novaceki** at approximately zone 40, near the middle of the Arroyo Seco local faunal zone. The subsequent appearance of several more mesic taxa (such as the gerrhonotine and the skink) after the disappearance of all iguanine genera may be an indicator of regional extinction followed by replacement. Argument for environmental change is strengthened (albeit untestable) by comparison with the stratigraphic distribution of the mammalian taxa. Near zone 40, a discontinuity in taxonomic composition, signified by several first and last appearances, caused Downs and White (1968) to place the boundary between the Arroyo Seco and Vallecito Creek local faunas at approximately zone 45.

However, sampling factors may bear on the apparent temporal pattern of lizard fossil occurrence. Fossil materials in the lower part of the section (Layer Cake and lower Arroyo Seco local faunal zone) are large, nearly complete specimens (primarily skulls), collected by traditional paleontologic methods of surface prospecting. More dense concentrations of bone, higher in the section, allowed some localities to be screen washed. Screen washing produced several taxa of small lizards that are not represented in the lower part of the section.

This sampling bias may explain the absence of many taxa low in the section but does not account for the absence of Arroyo Seco local fauna taxa in the Vallecito Creek local fauna. The apparent extinction of two large, phylogenetically allied, herbivorous taxa correlates with the regional first occurrence of several mammalian taxa that suggest a spread of grassland and savanna habitat (Becker and White, 1981). The apparent earlier faunal discontinuity (zone 40 as opposed to zone 46) in lizards relative to mammals is probably also a sampling artifact because lizards are not as common as mammals or found at as many localities. This pattern may characterize a regional change in floral composition reflecting climatic effects.

## COMPARISON OF FAUNA

The Anza Borrego assemblage is the most diverse Neogene lizard assemblage yet collected (Table 1), but it shares only minimal taxonomic similarity with temporally bracketing assemblages. Problems with this comparison are two-fold. The limit of morphologic resolution provided by many lizard fossils is at the subfamilial level or above. Considering that most of these higher level taxa have temporal ranges extending through most of the Neogene, such comparisons are of little value. Second, late Tertiary lizard assemblages are taxonomically depauperate with only a few specimens representing a small number of taxa. A characteristic late Tertiary assemblage from western North America includes a *Eumeces*-like skink, one or two sceloporines, iguanids, and an *Elgaria*-like gerrhonotine, limiting the range of possible taxonomic comparisons.

In the immediate vicinity of the Anza Borrego region are several bracketing fossil assemblages. Approximately 100 km north of the Anza Borrego are the outcrops of the Barstow Formation (Barstovian), which has produced a few fossil lizard taxa (Lindsay, 1972). Aside from the typical Neogene lizards, the Barstow Formation has produced an unnamed xantusiid similar to *X. downsi** (Gauthier, pers. comm.). This same xantusiid is also present in the younger Dove Springs Formation (Clarendonian), in conjunction with the monotypic *Paragerrhonotus ricardoensis* (Estes, 1963b) and the typical Neogene assortment of sceloporines, anguids, and skinks (Whistler, pers. comm.).

In the Cajon Formation (San Bernardino County, California; Barstovian-Hemphillian) a small gerrhonotine and some fragmentary sceloporine material have recently been collected (pers. obs.). The Wye local fauna of similar age, in the Crowder Formation of San Bernardino County, California, has also produced a typical Neogene suite of lizard fossils (pers. obs.).

The Tesuque Formation of New Mexico contains a few very interesting unstudied lizard specimens, including a gerrhonotine, a small iguanid of uncertain affinities, and an unnamed iguanine (Norell and de Queiroz, in prep.). The preservation of this material is reminiscent of that from Anza Borrego.

No contemporaneous lizard assemblages exist in the immediate Anza Borrego area. Outside the region, however, several localities from the southern Great Plains produce Blancan land mammals associated with lizard fossils. Beck Ranch (Rogers, 1976) has produced several taxa including a gerrhonotine, three sceloporines, a *Phrynosoma* species, two teiid species, and two skink species. Because comparisons in Roger's study were geographically limited, the identifications of these taxa to the species level is dubious. The best known Late Pliocene assemblage from the Great Plains occurs at Rexroad Kansas (Taylor, 1941; Hibbard, 1941). This deposit has produced lizard fossils from several localities, but it shares no specific taxa with the Anza Borrego assemblage.

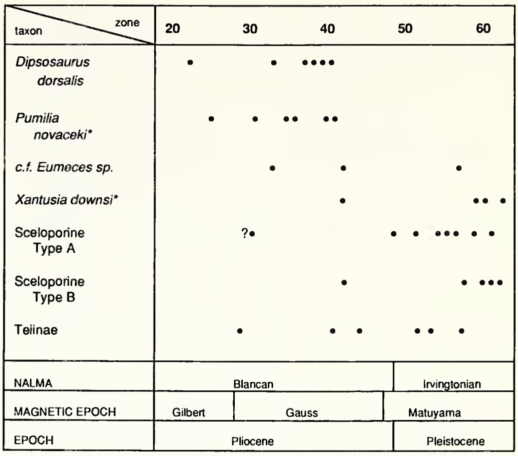

**Figure 17.** Stratigraphic occurrence of Anza Borrego lizard fossils.

The Curtis Ranch locality (Lammers, 1970; Harrison, 1972) in southern Arizona is the only temporally equivalent deposit in the region. It has produced numerous, mostly unstudied, lizard fossils, with several modern taxa (pers. obs.).

Taxa from the Anza Borrego Desert are only marginally comparable to specimens from other localities of equivalent age. Not until the Middle or Late Pleistocene do good samples of lizard fossils occur. Unsurprisingly, these show a distinctly modern assortment of taxa. The Anza Borrego fauna shows a high level of endemism that mirrors the condition of the extant lizard fauna. The high endemicity may be due more to the remarkable preservation of the Anza Borrego material than to its taxonomic uniqueness. Unlike mammals, lizards typically do not show a wide range of easily recognizable dental characteristics and are poorly represented fossils. Nevertheless the striking similarity of the Anza Borrego fossil assemblage with the Anza Borrego extant fauna is in contrast with the mammalian taxa, for which relatively few extant genera occur in the fossil deposit. This pattern is typical of regional Pleistocene localities (Norell, 1986) and may indicate the relative greater age of lizard genera compared to mammals (Peabody and Savage, 1958).

## CONCLUSIONS

Unlike many fossil lizard specimens, the outstanding preservation of the Anza Borrego material allows taxonomic referrals to be made with confidence. The taxonomic analysis indicates that Late Pliocene and Early Pleistocene regional assemblages were dominated by membrs of the Iguanidae, as is the modern fauna. Many of the fossil genera, including *Dipsosaurus, Phrynosoma, Gambelia,* cf. *Eumeces,* and *Ameiva-Cnemidophorus,* are ubiquitous lizards in the Anza Borrego region today. Additionally, the metaspecies *Xantusia downsi** is closely related to local *Xantusia* species. The only demonstrably extralimital taxon, in the sense that no close cladistic relatives occur regionally, is the metaspecies *Pumilia novaceki**, which is the sister-taxon of *Iguana.* The northernmost occurrence of the genus *Iguana,* in the riparian gallery forests of western Mexico, coincides with a lizard assemblage that is similar at the generic level to the lizard assemblage described here and may indicate a region of similar habitat to Anza Borrego during Late Pliocene time.

This analysis elucidates the difficulty in assigning specimens to species or genera when cladistic structure and character hierarchies within the groups are unknown or when material has been diagnosed on the basis of characters that are rarely preserved in fossil specimens. Failure to recognize these difficulties has resulted in the identification and allocation of many lizard fossils to taxa on the basis of plesiomorphy or geographic location. Others have simply been overinterpreted. This problem causes the study of regional evolutionary patterns and distributions to be difficult and imprecise. Unless the pattern of taxa through time is portrayed as a hierarchic branching of monophyletic taxa, the data are not applicable to these questions. These problems indicate that a better understanding of the temporal and regional history of lizards will not necessarily require a better fossil record—only a rigorous reinterpretation of the existing one, cast within a framework of living taxa.

The Anza Borrego lizard assemblage is taxonomically the most diverse Neogene assemblage yet documented. The analysis of these specimens indicates that many taxa occupying the area today have a long history in the region, because much of their phylogenetic proliferation was previous to the deposition of the Palm Springs Formation. This agrees with other findings that generic radiation of many of the region's extant genera occurred relatively early and may be associated with the origin of the Madro-Tertiary geoflora in the Early Miocene (Axelrod, 1958; Peabody and Savage, 1958; Savage, 1960, 1967). The early occurrence of many genera and their persistence in the fossil record indicates that the diverse lizard fauna of southwestern North America has developed *in situ,* rather than arisen as the product of recent immigration (*contra* Tihen, 1964).

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# The Feeding Mechanism in the Pleistocene Ground Sloth, *Glossotherium*

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# THE FEEDING MECHANISM IN THE PLEISTOCENE GROUND SLOTH, *GLOSSOTHERIUM*

VIRGINIA L. NAPLES[1]

**ABSTRACT.** The masticatory musculature in *Glossotherium* Owen, 1840, was reconstructed from study of the scars of muscle origin and insertion. Details of muscle architecture and hypotheses of function were deduced through comparison with the extant tree sloths, *Bradypus* Linnaeus, 1758, and *Choloepus* Illiger, 1811. Examination of dental wear facets has shown that *Glossotherium* had an anteromedially directed masticatory power stroke, comparable with most other mammals. As in other sloths, the shape and orientation of the zygomatic arch and its processes suggest a biomechanical advantage for muscles of the masseter complex. Although the anterior caniniform teeth in *Glossotherium* are short, they require a precise dorsoventral occlusal relationship, facilitated by a craniomandibular joint, at or near the level of the cheek tooth row as seen in *Choloepus*. The masticatory muscles in *Glossotherium* show a distribution of primitive and derived characters different from that of tree sloths and *Nothrotheriops shastense* Sinclair, 1905. A greater number of cranial morphological characters in *Glossotherium* are more similar to those of *Choloepus* than to *Bradypus*, although this probably reflects similar constraints placed upon masticatory architecture by elongate caniniform teeth. Derived characters, including (1) inflated cranial sinuses, (2) elongated uninflated pterygoid flanges, and (3) zygomatic arch process size and orientation, do not resemble those of the tree sloths or of *Nothrotheriops shastense*.

## INTRODUCTION

The sloths are divided into three large groups, the mylodontids, the megalonychids, and the megatheriids. The genus *Glossotherium* Owen, 1840, from the Pleistocene of North America is a member of the mylodontids. Of these sloths, the Mylodontidae are most likely to be monophyletic, as suggested by several character complexes that include cranial and mandibular morphology and dentition (Stock, 1925). Engelmann (1985) divided the Mylodontidae into three categories: (1) an unspecialized group that includes two genera, *Orophodon* Ameghino, 1895, and *Pseudoprepotherium* Hoffstetter, 1961; (2) the Scelidotheriinae, a group characterized by having a concave cuboid facet on the distal head of the astragulus and a slender, elongate skull and mandibles; and (3) the Mylodontinae, a group united by loss of the entepicondylar foramen of the distal humerus and by anteriorly broad snouts.

Of the five genera in the Mylodontinae, *Lestodon* Gervais, 1865, can be separated at the first node of Engelmann's (1985) cladogram, based upon dental characters, and *Thinobadistes* Hay, 1919, at the second node, based upon cranial and astragular differences, from the remaining three genera. The genera *Mylodon* Owen, 1840, *Paramylodon* Brown, 1903, and *Glossotherium* have been confused for one another in the literature (Stock, 1925; Hoffstetter, 1952). The tendency to lose the upper first tooth in *Paramylodon* makes assessment of the phylogenetic distance between *Paramylodon* and *Mylodon* (which lacks the anterior teeth entirely [Reinhardt, 1879; Stock, 1925]) difficult. *Paramylodon* has also been included within *Glossotherium* at some times, giving *Paramylodon* an unusually wide range of morphologic diversity. Hoffstetter (1952) and Engelmann (1985) observe that morphologic differences between *Glossotherium* and *Paramylodon* need to be defined to clarify their relationship. Some confusion exists as to the proper generic name for the North American late Pleistocene mylodont, and the use of the name *Glossotherium* reflects the current convention, following Kurten and Anderson (1980), and is not a taxonomic decision based on the present study.

The purpose of this study is to identify interdependent cranial characters and character complexes among *Mylodon, Paramylodon,* and *Glossotherium* by analyzing functional constraints on feeding in *Glossotherium*. An attempt to ascertain the limits of variability of the components of each cranial morphological complex will also be made. Definition of the interrelationships of characters and character complexes should show the biomechanical constraints upon variation among them, and thus establish physical boundaries that could not be exceeded for the performance of a given function. Any variation beyond these parameters would demonstrate that the function of the character or complex differed from predictions based upon biomechanical principles and, therefore, could be assumed to reflect a different habitus or different selective pressures from those acting upon the rest of the group, and would suggest a more distant relationship within the Mylodontinae.

The present study provides the first step toward

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[1] Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115-2861.

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**Table 1. Terminology and abbreviations used in this study.**

Ligaments

Postorbital ligament = POL
Zygomatic arch ligament = ZAL

Joints

Craniomandibular joint = CMJ

Muscles

*M. masseter superficialis* = *M.m.s.*
*M. masseter superficialis*, part 1 = *M.m.s.*—1
*M. masseter superficialis*, part 2 = *M.m.s.*—2
*M. masseter superficialis*, part 3 = *M.m.s.*—3
*M. masseter superficialis*, part 4 = *M.m.s.*—4
*M. masseter superficialis*, part 5 = *M.m.s.*—5
*M. masseter profundus* = *M.m.p.*
*M. temporalis superficialis* = *M.t.s.*
*M. temporalis superficialis pars* = *m.z. zygomaticomandibularis*
*M. pterygoideus lateralis*, upper division = *M.p.l.u.*
*M. pterygoideus lateralis*, lower division = *M.p.l.l.*
*M. pterygoideus medius* = *M.p.m.*

resolving questions concerning the relationships among *Paramylodon, Glossotherium,* and *Mylodon.* Functional analysis of the cranial characters and identification of character complexes subject to common biomechanical constraints should distinguish structural requirements that permit function from character or complex state differences arising from genetic inheritance. Comparison of functional characters in *Glossotherium,* for which the biomechanical limits will be demonstrated here, with those of *Mylodon* and *Paramylodon* will also show the difference between characters and complexes that have converged in appearance because of biomechanical requirements, and those which reflect a common genetic basis.

One of the goals of this study is to distinguish primitive from derived characters and character complexes, in order to establish the evolutionary sequence in which functional changes occurred in *Glossotherium.* Determination of polarities in cranial character complexes in *Glossotherium* will also provide insight into the sequence of evolutionary changes that split the *Paramylodon–Glossotherium–Mylodon* group. Hypotheses of cranial character and character complex function generated exclusively from observations of fossil crania and dentitions cannot be confirmed experimentally. However, a more precise model of functional patterns in fossil animals can be constructed when based upon comparison to characters and character complexes of a functional model tested experimentally in extant animals. Therefore, the *Glossotherium* crania have been compared to those of the tree sloths *Bradypus* and *Choloepus,* wherein cranial soft tissues have been studied and hypotheses of function have been tested experimentally (Naples, 1982, 1985a). Although *Bradypus* and *Choloepus* are both arboreal, they are probably not closely related; they show many differences in cranial morphology (Sicher, 1944; Naples, 1982, 1985a, 1985b, 1986) and have been aligned with the megatheriids and megalonychids, respectively (Patterson and Pascual, 1972; Webb, 1985; Wetzel, 1985). Thus, comparison of *Glossotherium,* a mylodontid, with members of each of the other two sloth families will show the pattern of the distribution of characters and complexes among the three lineages, and contribute to the determination of primitive or derived status for those characters. Comparison of osteological characters in *Glossotherium* with those of the extant tree sloths permits a detailed reconstruction of the cranial soft anatomy in the fossils, based upon the assumption that similar features are homologous and are subject to similar functional constraints (Naples, 1987). Accordingly, the cranial musculature in *Glossotherium* has been reconstructed to be similar in pattern of differentiation and action to that of the tree sloths. Morphological comparison of *Glossotherium* with *Nothrotheriops* will increase understanding of the dietary habits, masticatory patterns, and biomechanical constraints on cranial function in *Glossotherium.* The dietary habits are well known for *Nothrotheriops,* and its cranial morphology has been reconstructed (Hansen, 1978; Naples, 1987). *Nothrotheriops* and *Glossotherium* are both megatheriid ground sloths present in the asphalt seeps at Rancho La Brea.

## MATERIALS AND METHODS

Specimens of *Glossotherium* examined, and the collections in which they are housed, are listed in Table 1. Cranial osteological characters studied include attachment areas of muscles and the position and orientation of cranial sutures. The relative size and shape of the craniomandibular joint and the mental symphysis were also considered because of their effects upon the pattern of masticatory movements, and the relative size, structure, and placement of the muscles of mastication. Significant cranial characters and character polarities were determined based upon comparison with the Recent tree sloths, *Bradypus* and *Choloepus,* and the megatheriid sloth, *Nothrotheriops.* Abbreviations of terms used in this study are listed in Table 2.

Dental features were analyzed to determine degree of tooth wear, tooth wear patterns, and the path of mandibular movement, based upon techniques developed by Greaves (1973), Rensberger (1973), and Costa and Greaves (1981). Occlusal relationships were deduced from examination of "cusps" formed by wear according to the path of mandibular motion.

Cranial muscles were reconstructed based upon dissections of tree sloth masticatory muscles (Windle and Parsons, 1899; Sicher, 1944; Naples, 1985a). The muscle terminology used here is consistent with that developed during other studies of Recent and fossil sloths (Naples, 1985a, 1985b, 1986, 1987). Muscle and muscle segment identifications in tree sloths were determined by tracing innervations. Scars located on osteological elements indicating muscle origin and insertion accurately predict the limits of muscle size and general structure in tree sloths;

Table 2. Specimens examined in this study. Specimens belonging to the Hancock Collection (HC) are so designated. The specimen from the American Museum of Natural History is a juvenile.

| Specimens of *Glossotherium* | | | |
|---|---|---|---|
| **Skulls** | **Mandibles** | | |
| Page Museum | Page Museum | | |
| LACMHC 1717-12 (=693) | LACMHC 718-3 | | complete |
| LACMHC 1717-9 (=694) | LACMHC 1719-1 | | complete |
| LACMHC 1716-3 (=695) | LACMHC 1718-RL-21 | (=842) | complete |
| LACMHC 1718-4 (=696) | LACMHC 1718-RL-31 | (=843) | complete |
| LACMHC 1717-32 | LACMHC 1718-RL-19 | (=844) | complete |
| LACMHC 1717-15 (=813) | LACMHC 1718-R1-22 | (=845) | complete |
| LACMHC 1717-25 (=814) | LACMHC 1718-RL-17 | (=846) | complete |
| LACMHC 1717-11 (=815) | LACMHC 1718-RL-18 | (=847) | complete |
| LACMHC 1717-13 (=816) | LACMHC 1718-RL-32 | (=848) | complete |
| LACMHC 1717-7 (=817) | LACMHC 1718-RL-20 | (=849) | complete |
| LACMHC 1717-8 (=818) | LACMHC 1718-RL-24 | (=850) | complete |
| LACMHC 1717-4 (=819) | LACMHC 1718-RL-26 | (=851) | complete |
| LACMHC 1717-2 (=820) | LACMHC 1718-RL-23 | (=852) | complete |
| LACMHC 1717-18 (=821) | LACMHC 1718-RL-25 | (=853) | complete |
| LACMHC 1717-3 (=822) | LACMHC 1718-RL-28 | (=854) | complete |
| LACMHC 1717-4 (=823) | LACMHC 1718-RL-27 | (=855) | complete |
| LACMHC 1717-5 (=824) | LACMHC 1718-RL-29 | (=856) | complete |
| LACMHC 1717-16 (=825) | LACMHC 1718-RL-30 | (=857) | complete |
| LACMHC 1717-17 (=826) | LACMHC 1718-L-5 | (=858) | left ramus |
| LACMHC 1717-20 (=827) | LACMHC 1718-L-34 | (=859) | left ramus |
| LACMHC 1717-21 (=828) | LACMHC 1718-L-35 | (=860) | left ramus |
| LACMHC 1717-28 (=829) | LACMHC 1718-L-14 | (=861) | left ramus |
| LACMHC 1717-29 (=830) | LACMHC 1718-L-36 | (=862) | left ramus |
| LACMHC 1717-23 (=831) | LACMHC 1718-L-10 | (=863) | left ramus |
| LACMHC 1717-22 (=832) | LACMHC 1718-L-15 | (=864) | left ramus |
| LACMHC 1717-26 (=833) | LACMHC 1718-L-16 | (=865) | left ramus |
| LACMHC 1717-24 (=834) | LACMHC 1718-L-12 | (=866) | left ramus |
| LACMHC 1717-24 (=835) | LACMHC 1718-L-18 | (=867) | left ramus |
| LACMHC 1717-31 (=836) | LACMHC 1718-L-13 | (=868) | left ramus |
| LACMHC 1717-30 (=1008) | LACMHC 1718-R-9 | (=869) | right ramus |
| LACMHC 1717-32 | LACMHC 1718-R-10 | (=870) | right ramus |
| | LACMHC 1718-R-5 | (=871) | right ramus |
| | LACMHC 1718-R-7 | (=872) | right ramus |
| | LACMHC 1718-R-8 | (=873) | right ramus |
| | LACMHC 1718-R-13 | (=874) | right ramus |
| | LACMHC 1718-R-14 | (=875) | right ramus |
| | LACMHC 1718-R-12 | (=876) | right ramus |
| | LACMHC 1718-R-11 | (=877) | right ramus |
| | LACMHC 1718-R-15 | (=878) | right ramus |
| | LACMHC 1718-R-16 | (=879) | right ramus |
| | LACMHC 1718-R-1 | | right ramus |
| Museum of Comparative Zoology | | | |
| 8429 skull | 8429 mandible | | |
| American Museum of Natural History | | | |
| 11270 skull | 11270 mandible | | |

therefore, similarly positioned muscles in *Glossotherium* have been assumed to be identical. Muscles reconstructed in *Glossotherium* are listed in Table 3.

The distance reflecting maximum gape in *Glossotherium* was quantified by the method of Herring and Herring (1974). This model allows an estimate of the length to which fibers of the masticatory muscles could be stretched. This length is determined by measuring the distance between the center of the scars of origin and insertion (Table 3). It has been demonstrated that long-fibered muscles (such as most tree sloth masticatory muscles) function under different biomechanical constraints than do short-fibered muscles (Gans and Bock, 1965; Alexander, 1968; Gans, 1982). These features therefore

**Table 3. The cranial muscles, divisions, and abbreviations used in this study and the amount of stretch of each muscle segment when the mouth is opened to various degrees of gape. Multipinnate muscles may stretch up to two times their resting length without incurring damage; therefore, only stretch factors over 2.00 would be limiting. For *Glossotherium* the *M. masseter superficialis,* part 5, could then be overstretched at gapes greater than 22 degrees, with the *M. pterygoideus medius* and *M. zygomaticomandibularis* only slightly less limiting. The lowest gape at which a muscle could be overstretched is italicized.**

| | | Degrees of gape | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Muscle | Divisions | 22 | 23 | 24 | 25 | 30 | 35 | 40 | 45 |
| *M. masseter superficialis* | part 1 | — | — | — | 1.21 | 1.24 | 1.27 | 1.29 | 1.31 |
| *M. masseter superficialis* | part 2 | — | — | — | 1.14 | 1.15 | 1.16 | 1.17 | 1.17 |
| *M. masseter superficialis* | part 3 | — | — | — | 1.26 | 1.30 | 1.34 | 1.37 | 1.40 |
| *M. masseter superficialis* | part 4 | — | — | — | 1.46 | 1.46 | 1.64 | 1.72 | 1.80 |
| *M. masseter superficialis* | part 5 | 1.97 | ***2.03*** | 2.07 | 2.12 | 2.38 | 2.64 | 2.90 | 3.17 |
| *M. masseter profundus* | — | — | — | — | 1.06 | 1.07 | 1.09 | 1.10 | 1.12 |
| *M. temporalis superficialis* | — | — | — | — | 1.67 | 1.81 | 1.94 | ***2.08*** | 2.21 |
| *M. temporalis superficialis pars zygomaticomandibularis* | — | — | — | — | 1.68 | 1.84 | ***2.01*** | 2.18 | 2.36 |
| *M. pterygoideus lateralis* | upper division | — | — | — | 1.38 | 1.49 | 1.61 | 1.75 | 1.88 |
| *M. pterygoideus lateralis* | lower division | — | — | — | 1.30 | 1.39 | 1.49 | 1.60 | 1.72 |
| *M. pterygoideus medius* | — | — | — | — | 1.76 | 1.92 | ***2.03*** | 2.25 | 2.41 |

maximize the accuracy of predictions by this model. Masticatory muscle origin and insertion scars in *Glossotherium* were similar to those of tree sloths, suggesting that this method is also accurate for predicting maximum gape in this extinct species. The distance to which a muscle fiber can stretch without damage is approximately 1.4 times the resting length of the fibers for parallel fibered muscles, and approximately twice the resting length for multipinnate fibered muscles (Carlsöö, 1942). The equation used by Herring and Herring (1974) to predict the distance to which a muscle segment must stretch to achieve a given angle of mandibular rotation is:

$$\left(\frac{L^2}{l}\right) = \frac{a^2 + b^2 - 2ab\cos(\theta + \phi)}{a^2 + b^2 - 2ab\cos\theta}.$$

The stretch factor for each muscle (ratio L/l) is the positive square root of the equation. The values of the variables are: a = length from the muscle origin to the craniomandibular joint (CMJ), b = length from the insertion to the CMJ, $\phi$ = the angle between a and b, L = length of the muscle with the mandible closed, and l = the length of the muscle with the mandible opened to angle $\theta$.

## RESULTS

### CRANIAL OSTEOLOGY

A suite of osteologic characters distinguishes sloth crania from those of other mammals: (1) a reduced edentulous premaxilla loosely bound to the maxilla; (2) lengthy maxillae; (3) a persistently growing adult dentition reduced in tooth number, complexity, lacking enamel, and lacking a deciduous dentition; (4) zygomatic arches often incomplete; (5) elaborated descending and often ascending zygomatic arch processes; (6) pterygoid bones showing elongate flanges and/or inflated sinuses; (7) elaborate frontoparietal sinuses; (8) fused mandibular symphyses; and (9) an elongate predental mandibular spout. All sloths show some of these characters, although none possess all, and the distribution differs among the tree sloth lineages (Mylodontidae, Megalonychidae, and Megatheriidae). Additionally, each character may vary in structure, both within and between sloth groups. Although many authors (Stock, 1925; Winge, 1941; Simpson, 1945; Romer, 1966; Patterson and Pascual, 1972; Engelmann, 1985; Webb, 1985) have proposed phylogenetic relationships among sloths, few studies have investigated the functional implications of sloth cranial structure. Only cranial characters that contribute to the understanding of structural–functional complexes and evolutionary relationships in *Glossotherium* have been included here.

#### Premaxilla and Predental Spout (Fig. 1A, B)

Few specimens of *Glossotherium* have the premaxillae *in situ.* They are arrowhead-shaped, reminiscent of those found in *Bradypus.* The two elements are fused at the midline posteriorly and are loosely bound to the maxilla. In all large adult specimens a gap is present between the premaxilla–maxilla articulation, except midventrally, where the posteriorly projecting premaxillary process fuses with a V-shaped notch between the left and right maxillae. The body of the premaxilla is thickened by a dorsal ridge running along the "sides" of the arrowhead. Anteriorly, the premaxillae show a transverse groove, probably for attachment of nasal cartilages extending farther anteriorly. The presence of large nasal cartilages is suggested by the large nasal openings and a widely flaring predental spout that projects anteriorly, which is close to the length of the premaxillae (Fig. 1A–C, E). Tree sloths have large nasal cartilages along with thick, flexible upper lips that extend the nasal region anteriorly and slightly beyond the predental spout. A thick, flexible upper lip is postulated for *Glossotherium.*

### Postorbital Process

Sloths lack a complete postorbital bar, and typically the postorbital process is small. In *Glossotherium,* the process is broad and thick, inflated by the underlying frontal sinus, and is an elaboration of a ridge continuing posterodorsally from the eminence at the origin of the jugal, consisting of two rounded processes that project laterally. The process which lies more posteriorly is larger and sharper, with a ridge that continues posterodorsally to fade into a broad, flattened area of the frontal that is underlain by the frontal sinus. Both projections may have served as sites of attachment for the postorbital ligament.

### Cranial Sinuses

An extensive frontoparietal sinus network is present in *Glossotherium.* Sectioned or partially eroded skulls (Stock, 1925) indicate that the sinuses are divided by bony partitions into chambers of varying size and shape. Both tree sloths have frontal sinuses. These sinuses also extend above the parietal area in *Choloepus;* however, they lack bony partitions (Naples, 1982). The sinuses increase frontal bone surface area and, in *Glossotherium* and *Choloepus,* the parietal area is inflated by distinct parietal sinuses. *Glossotherium* and *Choloepus* lack a sagittal crest; however, cranial sinuses increase the surface area that *M. temporalis* and, in some cases, the neck muscles inserting upon the occiput can occupy. In *Glossotherium,* the parieto-occipital suture is thickened and flares laterally, forming a lambdoidal crest that widens the occiput by approximately one-third. This effectively increases the area for insertion of the head-controlling and postural neck muscles.

### Occiput and Occipital Condyles

The lateral occipital protuberance and crest form a narrow raised ridge from the sagittal suture to the foramen magnum. Because the lambdoidal crest is also raised, the occipital plane appears concave. The entire area is rough with dorsoventral ridges. The occiput is slanted, and the occipital condyles project posteriorly. The condyles are widely separated, strongly convex, rounded triangles with a horizontal long axis. The foramen magnum is relatively small and round, and large ventral and lateral openings for the jugular foramina are present.

### Structure of the Craniomandibular Joint (CMJ; Fig. 1C–I)

In *Glossotherium,* the glenoid fossa is poorly defined, with a shallow, ventrally facing, mediolateral depression at the condylar articulation on the squamosal process. A round depression occurs on the vertical wall at the thickened pterygoid flange base, ventral to the temporal-pterygoid suture, and receives a distinct medial facet of the mandibular condyle. The mandibular condyle is wider mediolaterally than anteroposteriorly, with a weakly defined dorsal surface that is poorly separated from the condylar notch anteriorly. Laterally, the condyle flares slightly. In addition to the main broad facet, a smaller anterior facet is present, separated by a curved ridge trending posterolaterally. Medially, there is a vertical round face, separate and angled at between 80 and 90 degrees from the horizontal dorsal condylar facet; the condyle projects farther medially than laterally relative to the ascending ramus of the coronoid process. This glenoid fossa and mandibular condyle structure indicates that condylar movement was unrestricted anteroposteriorly and laterally, but strictly limited medially.

In *Choloepus,* the CMJ is generally similar to that of *Glossotherium,* although the articular surfaces are more sharply defined, except for the medial vertical facet. In contrast, the long axis of the CMJ in *Bradypus* is anteroposteriorly oriented, and the base of the pterygoid flange is somewhat thickened, but lacks a medial face. In *Glossotherium,* which may have short caniniform teeth, the CMJ is approximately the same height as the cheek tooth row. *Choloepus,* which also has long caniniform teeth, has a CMJ level with the cheek tooth row, whereas *Bradypus,* which lacks elongate anterior teeth, has an elevated CMJ. The occlusal plane of the upper and lower tooth rows are equidistant from the CMJ in *Glossotherium* and other sloths (Naples, 1982, 1985a, 1987), insuring simultaneous occlusion and equal intercuspation along the length of the tooth row.

### Pterygoid Region

*Glossotherium* pterygoid morphology is unusual in comparison to other mammals (Stock, 1925; Turnbull, 1970). The bones are plate-like flanges, elongated ventrally, with a rounded inferior border and buttressed medial to the articulation with the medial condylar facet. The external surface is roughened, and shows scars for the origin of the medial pterygoid muscle. Other sloths (*Bradypus, Nothrotheriops*) have a similar pterygoid morphology, although the entire character complex associated with pterygoid development is unique to *Glossotherium* and other mylodont sloths.

### Palate

The palate in *Glossotherium* is widest anteriorly adjacent to the small caniniform teeth. It is thickened dorsoventrally by two ridges that continue anteriorly to the premaxillary suture. The palate tapers posteriorly, becoming narrowest between $M^3$ and $M^4$, widening again slightly at the rear of $M^4$. The entire palate is roughened with many pits; some are undoubtedly for foramina. It is strongly convex between $M^2$ and $M^3$ and flat or slightly concave anteriorly. A sharp midline ridge begins at the anterior concavity and ends anterior to $M^4$, where the palate exhibits a smooth V-shaped depression bounded laterally by sharp ridges. At the posterolateral edges of this V-shaped depression, the greater palatine foramina are large and accompanied by a row of smaller foramina along the edges of the maxillae that end anterior to the caniniform teeth. The choanae open in a V-shaped notch and are wider than the smooth part of the palate.

## CRANIAL LIGAMENTS

The three major cranial ligaments in sloths include (1) the postorbital ligament (POL), (2) an anterior–posterior ligamentous connection between the jugal and squamosal processes of the zygomatic arch (zygomatic arch ligament, ZAL), and (3) ligaments of the CMJ (Fig. 1A). In contrast to most other mammals, anterior and posterior processes of the zygomatic arch in the sloth skull are loosely apposed and were probably connected by a ligament.

### Postorbital Ligament

Based upon comparison with the tree sloths, a ligament covered the upper zygomatic arch of *Glossotherium.* It arose from the broad postorbital process and attached to a rounded process formed where the anterior surface of the ascending jugal process turns posteriorly, then continued superficially to the outer surface of the temporal musculature. The postorbital ligament was thick and completed a round orbit, separating the eye region superficially from the temporal fossa. In addition to the ligament covering the upper jugal process, attachment scars located posteriorly and medially on the lower half of the jugal notch and on the dorsal, lateral, and anteroventral surfaces of the broad, flat squamosal process indicate the presence of a large zygomatic arch ligament. This is reminiscent of the condition found in *Choloepus,* which has a more posteriorly directed upper jugal process than *Glossotherium* and an even clearer division of the two ligaments. In contrast, with a strongly vertical ascending jugal process, the POL and ZAL in *Bradypus* appear to be almost continuous.

In *Glossotherium,* as in tree sloths, the ZAL continues ventral to the apposed jugal and squamosal processes. In tree sloths, particularly *Bradypus,* this ligament is large. The zygomatic arch orientation in *Glossotherium* precludes a large ligament; however, an attachment scar is located on the ventral surface of the jugal notch, opposite an oval depression posterior to the broad, flat ventral area of the squamosal. These scars suggest that the zygomatic arch attachment was strengthened ventrally by a thickened, and perhaps separate, ligamentous band between jugal and squamosal.

### Ligaments of the CMJ

A medial ridge marks the limit of the glenoid fossa in *Glossotherium.* In general, the ridge is small and thin but becomes thicker and more prominent near the medial vertical facet. Muscle scars on the mandibular condyle are more pronounced, particularly medially and posterolaterally. Approximately 50% of the condylar head is medial to the coronoid process. The area for insertion of the two lateral heads of the pterygoid muscle is sharply defined and surrounded medially and ventrally by a prominent roughened ridge. This suggests that the lateral pterygoid attachments pierce the joint capsule as in other mammals. Tree sloths lack an articular disc. The extensive flat area of glenoid fossa–condyle articulation in *Glossotherium* suggests a similar absence. The glenoid surface in *Glossotherium* is much larger than the condyle area, suggesting that the CMJ capsule was loose and thin (except medially) and permitted extensive condylar movement. Although the glenoid fossa and condyle differ in shape, the capsule in both Recent genera of tree sloths is both thin and lax (Naples, 1985a).

## DENTAL MORPHOLOGY

Sloths have an ever-growing adult dentition, a reduction in the tooth number, and lack a deciduous dentition (Parker, 1885). This makes tooth homologies difficult to discern. Sloth teeth also lack enamel (Romer, 1966) and the cuspation pattern shown in other mammals. Typical tooth forms are oval, subrectangular, or elongate irregular ovoids. Anterior teeth are called caniniform (or chisel-shaped), and cheek teeth are termed molariform (Fig. 2A, B).

Upon eruption, the teeth are cone-shaped and only acquire their characteristic facet and "cusp" pattern with wear during the life of the animal (Naples, 1981, 1982). Each tooth has a perimeter of harder dentine and a softer dentine center, which explains the formation of central basins. In *Glossotherium,* the perimeter hard dentine layer is of approximately equal thickness on all aspects of the teeth, as in *Choloepus.* In contrast, the perimeter dentine layer on anterior and posterior faces is thicker than on lingual and labial faces in the megatheriids *Bradypus* and *Nothrotheriops* (Naples, 1982, 1987). Parker (1885) suggested that tree sloths also have a layer of cementum surrounding the teeth, but in many specimens this is indistinct. However, in *Glossotherium,* the cementum is obvious and surrounds all cheek teeth. Traces of cementum have also been found on the anterior caniniform teeth in some specimens.

The dental formula $(\frac{5}{4})$ in *Glossotherium* is the same as in tree sloths; however, the teeth are more elongate, more complicated in shape, and relatively larger than in *Bradypus* and *Choloepus* and occupy more space along the tooth row. Some *Glossotherium* specimens lack development of the caniniform teeth, giving them a reduced dental formula $(\frac{4}{3})$ as compared to the tree sloths, but loss of these teeth does not change the occlusal relationship of the molariform teeth. A description of tooth structure in *Glossotherium* has been presented by Stock (1925), although the pattern of wear facet formation and occlusal relationships were not discussed.

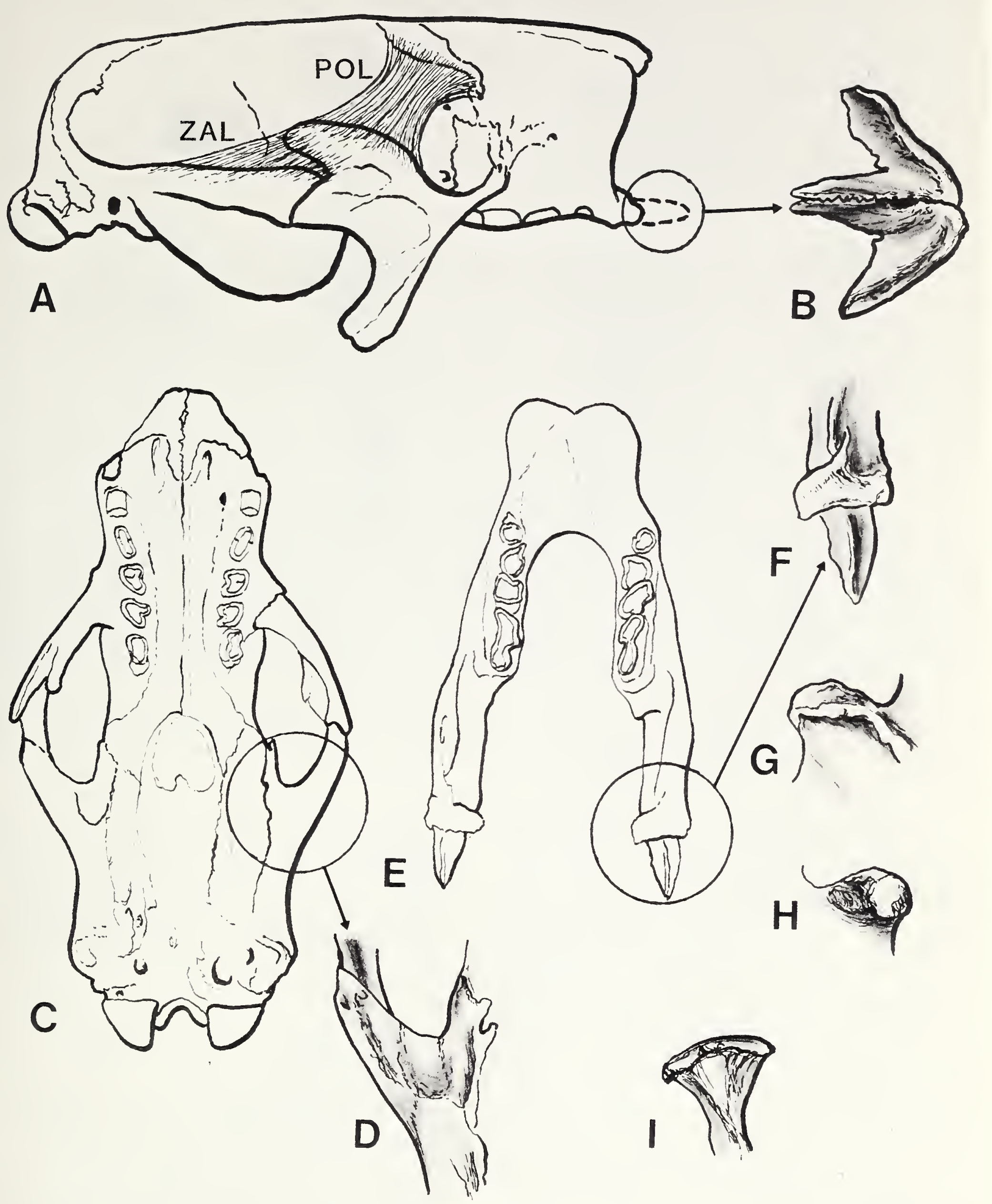

**Figure 1.** Views of the skull of *Glossotherium* (1A, lateral; 1C, ventral) and mandible (1E, dorsal view in occlusal position with 1C), and enlargements of regions of the skull (1B, premaxilla, dorsal view; 1D, glenoid fossa, ventral view) and mandible (1F, condyle, dorsal view; 1G, condyle, lateral view; 1H, condyle, medial view; 1I, condyle, posterior view). The ligaments of the zygomatic arch are reconstructed in 1A; the portion between the postorbital and upper zygomatic arch processes is called the postorbital ligament (POL), and the anterior–posterior connection between the jugal and squamosal processes of the zygomatic arch form the zygomatic arch ligament (ZAL) proper.

Sloths reverse the typical mammalian tooth occlusion order with the mandibular caniniform or chisel-shaped tooth anterior to the corresponding maxillary tooth. The maxillary cheek teeth also precede the mandibular cheek teeth by half a tooth length, a derived character shared with other sloths (Owen, 1842; Anthony, 1918; Stock, 1925; Hirschfeld and Webb, 1968; Naples, 1981, 1982, 1987).

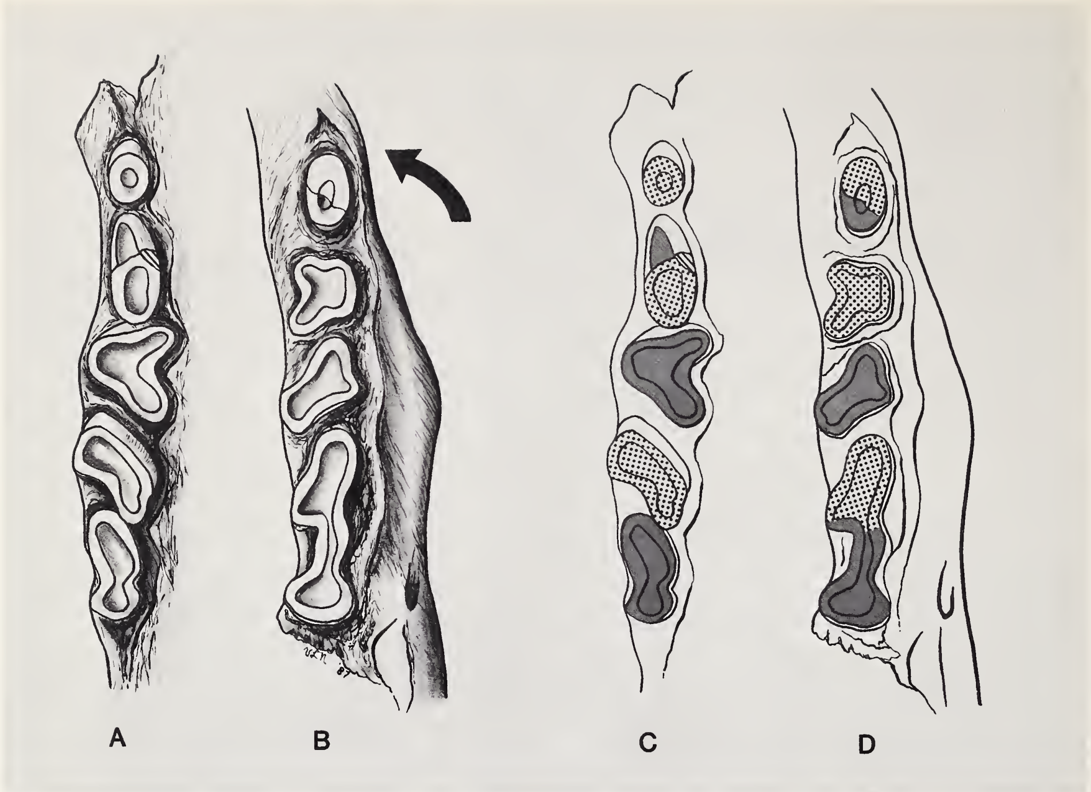

**Figure 2.** The right maxillary (A) and mandibular (B) dentition of *Glossotherium* (MCZ 8429) showing details of tooth structure. The arrow indicates the direction of mandibular masticatory movement. Dotted and shaded areas of the maxillary (C) and mandibular (D) dentitions show the occlusal relationship in *Glossotherium.* The diagonal striped areas in A and C indicate missing parts of the $M^1$.

*Glossotherium* shows the typical intercuspation arrangement seen in other sloths, with four maxillary molariform teeth occluding against three mandibular molariform teeth (Fig. 2C, D). The $M^1$ and $M^4$ have only one opposite occlusal surface in *Choloepus,* whereas the $M^2$ and $M^3$ each occlude with two mandibular cheek teeth. In megatheriids, in contrast, the $M^1$ may occlude with a posterior face of the anterior lower caniniform or chisel-shaped tooth (if present) and with the anterior face of the $M_1$. However, in megatheriids, the $M^4$ also occludes only with the $M_3$. In *Glossotherium* (a mylodontid), the $M^1$ occludes with $C_1$ and $M_1$ and the $M^4$ with the posterior aspect of the $M^3$. The $M^3$ has a more elongated anteroposterior axis than in other sloths studied here. Occlusion of the $M^1$ with more than one mandibular tooth requires the mandibular teeth to occlude in more than one position (Fig. 2C, D), which is true in tree sloths (Naples, 1982: fig. 15E–H). In tree sloths, the occlusal position for biting with the anterior teeth differs from the mandibular position required to appose the cheek teeth for chewing. However, the difference between the biting and chewing occlusal positions in *Glossotherium* is small, because the diastema separating the anterior caniniforms from the cheek tooth row is less pronounced.

The first maxillary tooth ($C^1$) in *Glossotherium* (when present) is oval in cross-section. It has a single posterior-facing occlusal surface that only wears against the anterior facet of $C_1$ (Fig. 2A). Stock (1925) described the outer hard dentine layer of $C^1$ as thicker than in the cheek teeth and that the occlusal face contained a slight depression.

The second maxillary tooth, $M^1$, is elliptical, with the long axis of the oval oriented approximately anteroposteriorly. The posterior aspect is directed more lingually. In contrast to Stock's (1925) observations, the anteroposterior tooth axis is shorter than that of $M^3$ (Fig. 2A). A basin, which is deeper posterolingually, occupies the tooth center; the entire occlusal surface is concave along the anteroposterior axis and occludes with the $M_1$. The hard outer dentine layer shows a slight anterior depression and a posterior ridge labially but is uniformly concave lingually. A distinct anterolabial wear facet occludes with the posterior facet of the $C_1$, wearing almost through the outer hard dentine layer but leaving a pointed "cusp" anteriorly. This may have provided a sharp-edged cutting surface.

The $M^2$ is triangular with two rounded lingual angles and one rounded labial angle. As noted by Stock (1925), the anterolingual lobe occludes with the posterolingual $M_1$ lobe; the labial and posterolingual $M^2$ lobes occlude with the $M_2$.

The $M^3$ is elliptical in *Glossotherium,* with convex lingual and concave labial edges. The long axis is oriented obliquely to the tooth row and the tooth is more lingual posteriorly. In contrast to Stock (1925), this tooth has the longest axis of any molariform tooth along the cheek tooth row. All $M^3$'s studied have a concave central basin that occludes with the anterior portion of the elongate $M_3$. The anterior basin portion in one $M^3$ contained two anomalous "islands" of hard dentine projecting above the surface.

The $M^4$ is kidney-shaped, with the long axis oriented anteroposteriorly. The anterior lobe is larger than the posterior, with a central basin continuous between the two. This tooth occludes with the posterior $M_3$.

The first mandibular tooth, $C_1$, was described (Stock, 1925); in addition, he discussed the presence or absence of $C^1$. As with $C^1$, the hard outer dentine layer in $C_1$ is thicker than in cheek teeth. The softer dentine basin is more deeply scoured labially on the anterior wear facet, and both hard and soft dentine areas bear wear striations along an anterolingual–posterolabial axis. This indicates that *Glossotherium* used an anteromedially directed masticatory power stroke similar to that observed in most other mammals (Hiiemae, 1978).

The $M_1$ is roughly triangular, with two rounded angles antero- and posterolingually and with one broader angle labially. Within the anterolingual lobe of the $M_1$, the transition from outer hard dentine to inner soft dentine is smooth and flush. The labial basin is deeper, and a step exists between hard and soft dentine, suggesting that the masticatory stroke in *Glossotherium* was anteromedially directed (Greaves, 1973; Rensberger, 1973; Costa and Greaves, 1981; Gordon, 1982; Naples, 1982; Fig. 2B). The anterolingual and labial occlusal surfaces and the posterolingual lobe are concave; however, the posterolingual lobe is separated by a rounded convex ridge located on the occlusal surfaces corresponding to wear facets created by the $M^1$ and $M^2$.

The $M_2$ has two lobes on the main anterolabial–posterolingual axis and a third, smaller posterolabial lobe. The concave surface and central soft dentine basin show a smooth transition from the hard perimeter dentine on the anterolingual aspect of the tooth and a deeper depression and step-like transition between soft and hard dentine on the posterolabial aspect of the tooth. Wear striations are discernible along an anterolingual–posterolabial axis.

The $M_3$ is the largest tooth in *Glossotherium*, with an anteroposterior long axis approximately twice the individual lengths of the other teeth. The elongated oval tooth shape is made irregular by two lingual lobes. The first lingual lobe is near the long axis midpoint, and the second is located at the tooth rear. As in other teeth, a central soft dentine basin is present; however, in $M_3$ it is nearly pinched off posterior to the anterior lingual lobe. The flush transition between hard and soft dentine is obvious in two places: along the anterolingual face and (lingually) posterior to the anterior lingual lobe. A step-like transition is present along much of the labial surface and posteriorly. The $M_3$ occludes with the $M^3$ and $M^4$ and the gap between occlusal surfaces results in retention of a sharp labial ridge opposite the anterior lingual lobe.

## CRANIAL MUSCULATURE

*Bradypus* and *Choloepus* show the typical trigeminal (mandibular branch, $V_3$) masticatory muscle innervation seen in other mammals. The innervation of the tongue, throat, and hyoid regions in the tree sloths also reflects the typical mammalian pattern. Nerve branch patterns could not be traced in *Glossotherium;* however, the foramen ovale and hypoglossal canal are in positions similar to those in the tree sloths.

## MASTICATORY MUSCLES

### Masseter Musculature (Fig. 3)

In sloths, as in many other mammals, the masseter musculature is complex and uniquely subdivided, retaining only superficial and deep portions (Windle and Parsons, 1899; Schulman, 1906; Toldt, 1906, 1907, 1908; Edgeworth, 1935; Turnbull, 1970; Sicher, 1944; Naples, 1985a). In Recent sloths, muscle scars indicating origin on the zygomatic arches and insertion on the mandibles show division of the superficial masseter into five parts by tendons and fascial sheets. In *Glossotherium* (Fig. 3), the scars are similar in relative size to those of *Bradypus* and *Choloepus,* although they differ in relative position and orientation from one or both.

***M. masseter superficialis,*** **Part 1 (*M.m.s.*—1; Fig. 3A, C, D, I).** In *Glossotherium,* part 1 arises from an oval depression on the lateral jugal surface anterior to the jugal notch. This segment is similarly positioned in *Choloepus* but not *Bradypus;* in the latter, the strongly vertical ascending jugal process orientation has permitted expansion and reorientation of the *M.m.s.*—1 origin. The fibers of *M.m.s.*—1 in *Glossotherium* pass posteroventrally to insert posterolaterally on the mandibular condylar process.

***M. masseter superficialis,*** **Part 2 (*M.m.s.*—2; Fig. 3A, C, E, I).** In *Glossotherium,* part 2 arises from a U-shaped depression ventral to the origin of *M.m.s.*—1. The fibers pass posteroventrally to attach on slightly more than the upper 50% of the mandibular angle. This arrangement is similar in tree sloths, where the more ventral segments of the *M.m.s.* partially cover the more dorsal ones, especially near the insertions.

***M. masseter superficialis,*** **Part 3 (*M.m.s.*—3; Fig. 3A, C, F, I).** In *Glossotherium,* part 3 arises from a large crescentic depression ventral to the origin of *M.m.s.*—2. This is the largest *M.m.s.* segment in *Glossotherium,* with an origin approximately twice the size of that of the *M.m.s.*—1 and *M.m.s.*—2.

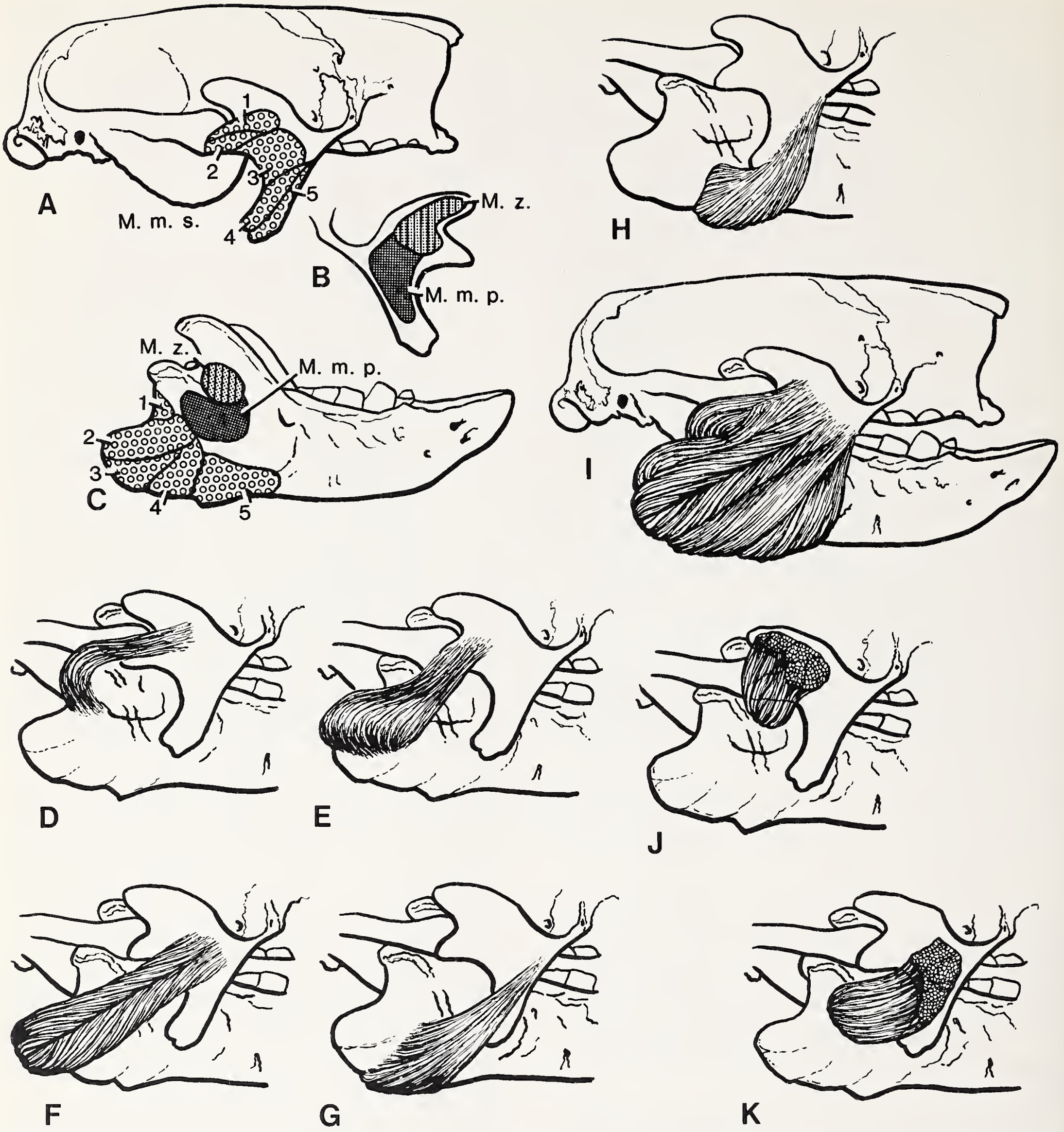

Figure 3. Skull and mandible of *Glossotherium* with the origins (3A), insertions (3C), and a reconstruction of the five segments of the *M. masseter superficialis* (*M.m.s.*). Each segment is individually rendered (3D–H) and reconstructed together (3I). Also shown are the origins (3B), insertions (3C), and a reconstruction (3J, K) of the *M. zygomaticomandibularis* (*M.z.*) and the *M. masseter profunda* (*M.m.p.*). The origin of the *M.z.* and *M.m.p.* is from the deep surface of the zygomatic arch, which is indicated as transparent (3J, K).

Roughening of the surfaces of origin and insertion suggest that this segment may have been fleshy and divided by several tendons. The fibers pass posteroventrally to a dorsal, ridged insertion on the mandibular angular process. In *Choloepus, M.m.s.*—3 is relatively smaller and inserts dorsal to the tip of the angular process. In *Bradypus*, the *M.m.s.*—3 is relatively larger than in *Choloepus* and encompasses the tip of the angular process. In *Glossotherium, M.m.s.*—3 is relatively larger than in tree sloths and inserts more ventrally on the ventral 40% of the angular process, entirely ventral to the tip. In *Glossotherium*, fibers trend posteroventrally in contrast to tree sloths, wherein *M.m.s.*—3 is approximately horizontal and parallel to the plane of the cheek tooth row.

***M. masseter superficialis,*** **Part 4 (*M.m.s.*—4; Fig. 3A, C, G, I).** In *Glossotherium*, part 4 originates from an elongate V-shaped depression trending posteroventrally on the descending jugal process, where a posterior notch occurs for muscle fiber and tendon passage. Part 4 inserts into a round mandibular depression bounded anteriorly and posteriorly by rough ridges but unmarked dorsally. In tree sloths, the muscle arises by a single tendon, is multipinnate, and is divided into many fascicles. This was the probable arrangement in *Glossotherium*, considering the large size and position of the *M.m.s.*—4 muscle scars.

***M. masseter superficialis,* Part 5 (*M.m.s.*—5; Fig. 3A, C, H, I).** In *Glossotherium*, part 5 originates from the most ventral depression on the descending jugal process, separated dorsally from the origin of *M.m.s.*—4 by a ridge. In contrast to *M.m.s.*—5 in tree sloths, this muscle in *Glossotherium* does not originate either from the anterior edge or extend onto the ventral surface of the descending jugal process. A rough knob at the tip of the descending jugal process (which probably is not an origin for fibers of *M.m.s.*) is at the posterior end of the ridge separating the origins of *M.m.s.*—4 and *M.m.s.*—5. *M.m.s.*—5 is more dorsoventrally oriented than *M.m.s.*—4. The bony knob reflects divergence in fiber direction between these segments as they pass dorsal and ventral to the knob. Fibers of *M.m.s.*—5 pass posteroventrally, about 60 degrees from horizontal, to insert into a ridge-bounded depression laterally and ventrally on the mandible. The depression is ventral to the posterior edge of $M^4$. The *M.m.s.*—5 forms the anterior and ventral cheek bulges in *Glossotherium*. In tree sloths, part 5 is complex, with many tendons and fascial planes. Pinnation of this segment would also have been important in *Glossotherium* to enhance the ability of the muscle to stretch (Herring, 1975). This anterior segment has the shortest distance from origin to insertion and, therefore, would limit the degree to which the sloth could gape.

The subdivisions, fiber arrangement, relative size, and overall line of actions of the *M.m.s.* in *Glossotherium* are similar to those of the tree sloths (Naples, 1985a). However, there is a greater range of orientation of segments in *Glossotherium* to affect the masticatory pattern.

***M. masseter profundus* (*M.m.p.;* Fig. 3B, C, I).** In *Glossotherium*, this muscle originates from a smooth depression on the medial surface of the descending jugal process. Fibers pass posteroventrally to insert into a smooth, ridge-bounded depression on the lateral surface of the mandibular ramus, which is anterodorsal to the superficial masseter. This muscle is probably thin and sheet-like as in tree sloths, with many fibers but few tendons extending from origin to insertion. Also, the space between the descending jugal process and the mandibular ramus in *Glossotherium* is narrow, although the origin and insertion of *M.m.p.* is relatively larger than in tree sloths. The *M.m.p.* has a more vertical origin site than in *Choloepus* and an anterodorsal line of action. These derived characters are also exhibited in *Bradypus* but for different structural reasons (Naples, 1985a).

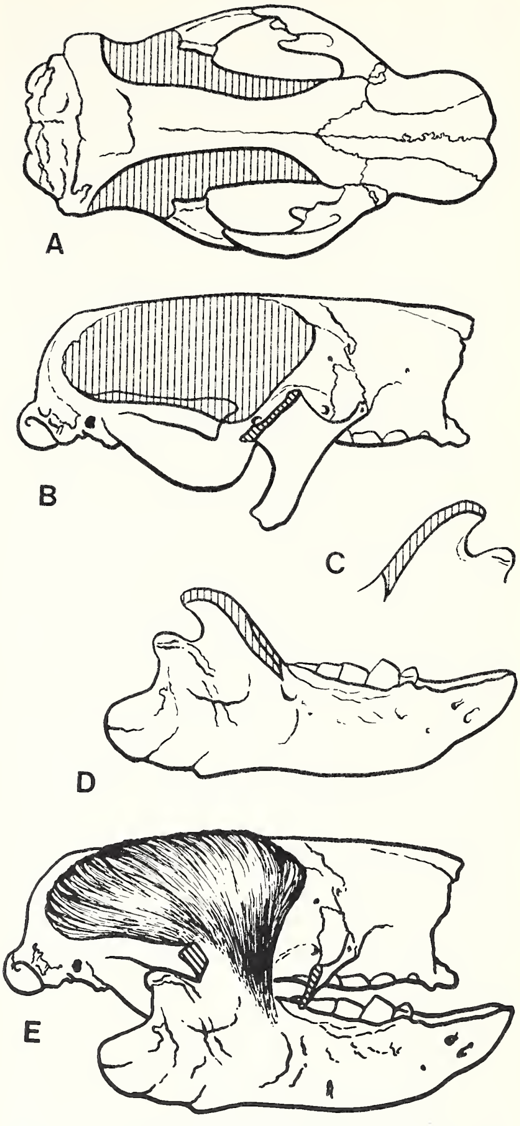

**Figure 4.** The origin (4A, dorsal view; 4B, lateral view), insertion (4C, medial view; 4D, lateral view), and a reconstruction of the *M. temporalis* (4E) in *Glossotherium*. In 4B and 4E, portions of the zygomatic arch have been removed (sections through the cut edges are designated by hatching).

***Temporalis musculature* (*M.t.;* Fig. 4).** In *Glossotherium*, the *M.t.* is large and thick, relative to that of tree sloths, and probably undivided. As is true of some other sloths, *Glossotherium* lacks a sagittal crest, but the dorsal origin of the *M.t.* is marked by a prominent roughened ridge—the parasagittal crest. The origin covers most of the dorsal and lateral aspects of the frontal and parietal bones (Fig. 4A, B) and the posterior one-third of the dorsal surface of the temporal squamosal process. The *M. t.* fills the depression between the parietal and squamosal process and passes ventrally anterior to these bones. Anteriorly, the origin continues from the postorbital process posteroventrally to a point immediately dorsal to the vertical ridge lateral to the optic canal. It then proceeds posteriorly to the anterior edge of the squamosal process to join the parietal bone. The muscle is a thick mass forming the posterior wall of the orbit. Fibers pass ventrally to attach to the roughened lateral, anterior, and medial surfaces of the coronoid process. The insertion area is small compared to the area of origin, indicating a fleshy origin for *M.t.* in *Glossotherium* and a tendinous insertion, as exhibited in other mammals (Turnbull, 1970; Naples, 1985a). The line of action of *M.t.* in *Glossotherium* is approximately 45 degrees to the plane of the tooth row and permits both mandibular elevation and retraction. The origin of the *M.t.* in *Glossotherium* is relatively more elongate than in either *Bradypus* or *Choloepus,* reflecting the relatively greater length of the skull (a primitive condition).

***M. zygomaticomandibularis*** **(=*M. temporalis superficialis pars zygomaticomandibularis; M.z.;* Fig. 3B, C, K).** In *Glossotherium,* this muscle arises from a smooth depression on the medial surface of the broad posterior and ascending jugal processes. In contrast to the tree sloths, especially *Bradypus,* the ZAL in *Glossotherium* provides no additional surface area for the muscle origin, even though it probably is relatively as large as in *Bradypus* and relatively much larger than in *Choloepus.* Fibers of *M.z.* in *Glossotherium* pass posteroventrally to insert into a ridge-bounded, smooth, oval depression at the base of the coronoid process, anterodorsal to the *M.m.p.* insertion. The *M.z.* has a relatively large origin and insertion, and the distance between the medial zygomatic arch surface and the mandibular ramus is short; therefore, as in tree sloths, this muscle is sheet-like and lacks tendinous divisions. The orientation of the *M.z.* in *Glossotherium* is posteroventral, similar to that in *Choloepus* and most other mammals, and is probably a primitive character.

### Pterygoideus Musculature (Fig. 5)

In general, these muscles in sloths are large relative to the pterygoid mass in other mammals (Toldt, 1906, 1907, 1908; Edgeworth, 1935; Turnbull, 1970; Naples, 1985a). However, the division of *M. pterygoideus* in sloths resembles that seen in other mammals.

***M. pterygoideus lateralis,*** **upper portion (*M.p.l.u.;* Fig. 5).** In *Glossotherium,* this muscle arises from a shallow, round depression high on the lateral aspect of the elongate pterygoid flange. The muscle passes posteroventrally to insert in a roughened depression on the anterior edge of the mandibular condyle, medial to the condylar notch. The origin and insertion are similar in tree sloths but less distinct in *Glossotherium.* The posteroventral line of action in *Choloepus* is typical of most mammals and also is seen in *Glossotherium* (Turnbull, 1970; Naples, 1985a). In contrast, this muscle is oriented posterodorsally in *Bradypus,* a derived character (Naples, 1985a), and is associated with ventral elongation of the pterygoid flanges. In tree sloths, the muscle is thick and fleshy and divided by few internal fascial planes, as is probable in *Glossotherium.*

***M. pterygoideus lateralis,*** **lower portion (*M.p.l.l.;* Fig. 5).** In *Glossotherium,* this muscle arises ventral to the *M.p.l.u.* from a larger and more oval depression. The line of action is slightly posterodorsal, differing from the *M.p.l.u.* The *M.p.l.l.* inserts into a roughened oval depression ventral to the *M.p.l.u.,* anteriorly on the condyle, and medial to the condylar notch. The *M.p.l.u.* line of action is reminiscent of *Bradypus* but not of *Choloepus.* In contrast to the tree sloths, with two similarly oriented *M.p.l.* segments, the lines of action of the two parts differ in *Glossotherium.* This is also exhibited in another ground sloth, *Nothrotheriops* (Naples, 1987). The upper and lower portions of the *M.p.l.* in *Glossotherium* are separate and relatively larger than those of *Choloepus* but similar to the relatively large muscles in *Bradypus.*

The *M.p.l.* in *Choloepus* pulls anteromedially, with a small vertical force component, whereas in *Bradypus* the *M.p.l.* pulls posterodorsally with a medial force component greater than the vertical force directed ventrally (Naples, 1985a, 1987). However, the *M.p.l.* functions similarly in both tree sloths. The downward force component (which would dislocate the mandibular condyle if large movements were involved) is canceled by the bony stop present only on the medial glenoid surface in *Bradypus,* presuming that the masseter and medial pterygoid muscles involved in this movement are active on both sides of the head simultaneously (Gysi, 1921; Herring *et al.,* 1979). In most mammals, the mandibular condyle slides downward upon opening (Carlsöö, 1942). Therefore, although different structurally from the typical mammalian arrangement, this mechanism prevents mandibular dislocation in tree sloths (Naples, 1985a, 1987). The medial glenoid surface in *Glossotherium* is a better bony stop than that in *Bradypus,* and therefore limits downward condylar movement more effectively (Fig. 5B). In *Glossotherium,* the dorsal and ventral force components of similarly sized, but differently oriented, *M.p.l.u.* and *M.p.l.l.* would cancel one another, resulting in a primarily anterior pull on the medial aspect of the condyle.

***M. pterygoideus medius*** **(*M.p.m.;* Fig. 5).** In *Glossotherium,* this muscle arises from a roughened oval depression, located posteroventral to the *M.p.l.l.* origin, on the lateral side of the elongated pterygoid flange (Fig. 5). The fibers pass posteroventrally, to insert into a large teardrop-shaped fossa posterior to the $M_3$ alveolus; the fossa is outlined by sharp ridges medially on the mandibular ramus and angle (Fig. 5). The *M.p.m.* in *Glossotherium* is relatively larger than in *Choloepus* and has a more anteroposterior line of action. This muscle has a mechanical advantage similar to that of *Bradypus* and a similar relative size (Fig. 5; Naples, 1985a). In tree sloths, the *M.p.m.* largely lacks internal fascial planes and has few ridges for tendon attachment, in contrast to the strongly roughened origin

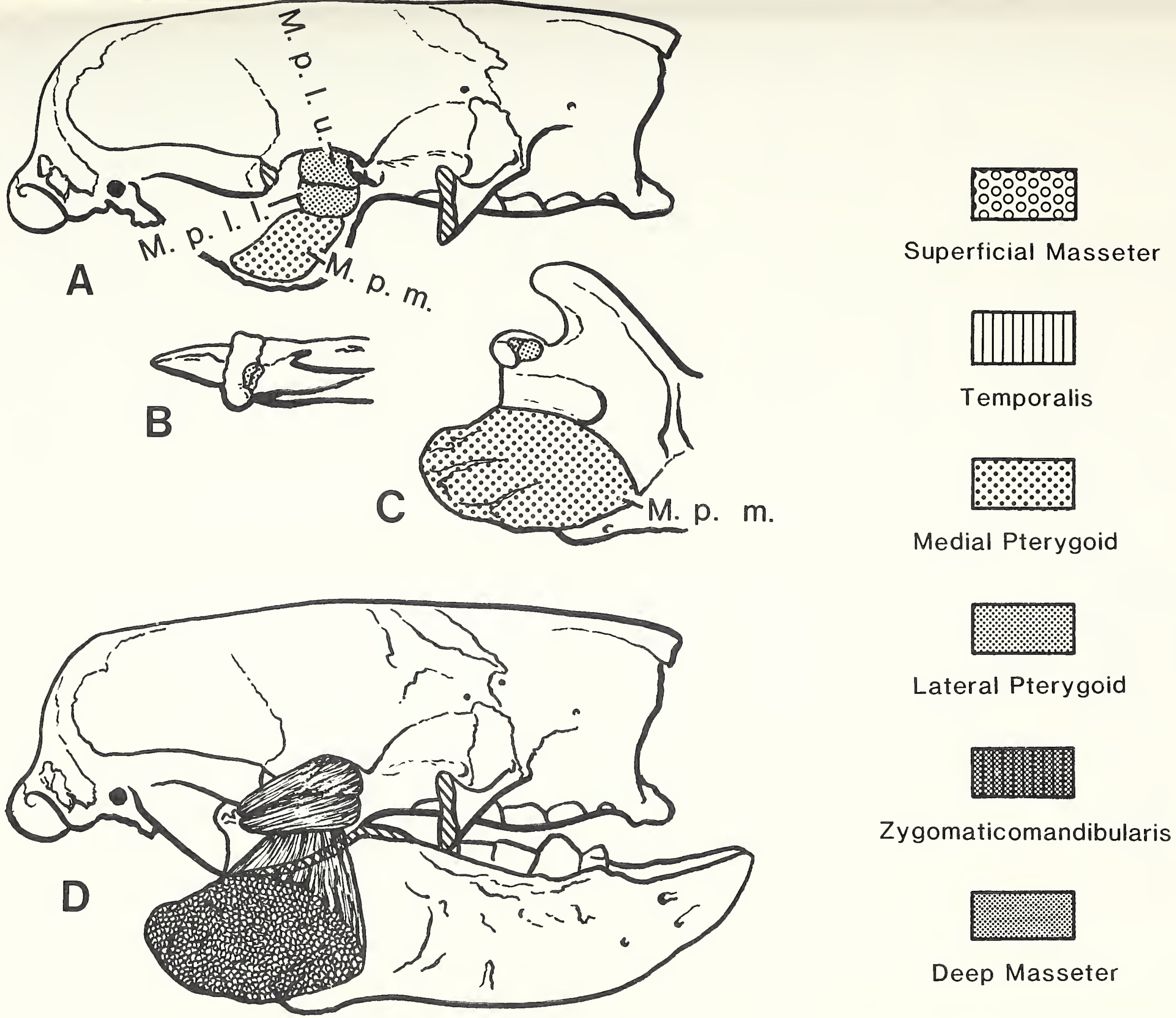

**Figure 5.** The origin (5A), insertion (5B), dorsal view; (5C), lateral view, and a reconstruction (5D) of the upper and lower heads of *M. pterygoideus lateralis* (*M.p.l.u.* and *M.p.l.l.*, respectively) and the *M. pterygoideus medius* (*M.p.m.*). The zygomatic arch and the coronoid process of the mandible have been removed (sections through the cut edges are designated by hatching) and at the site of insertion the mandible is shown as if it is transparent. A key to the muscle shading patterns for Figures 3–5 is shown at the right.

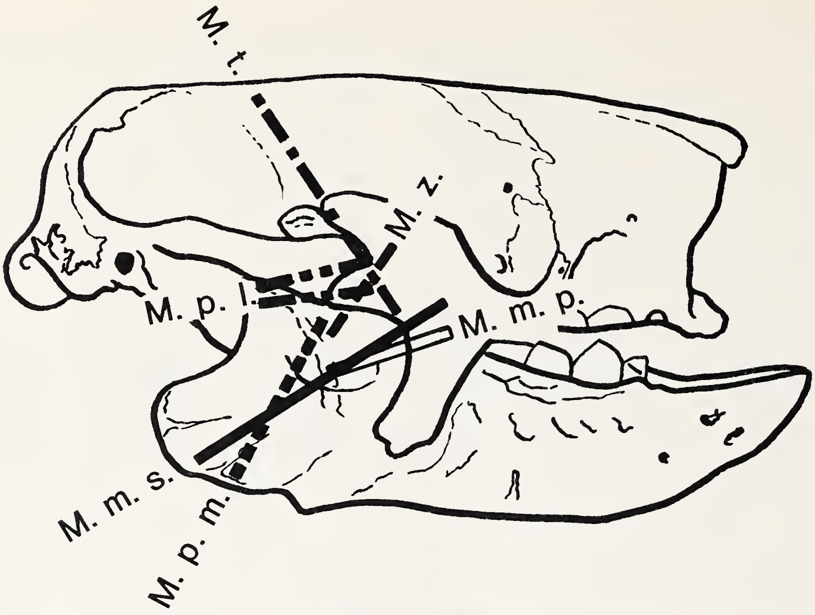

**Figure 6.** Lateral view of the skull and mandible of *Glossotherium* in occlusal relationship shows the lines of action of the muscles of mastication. Muscle abbreviations are as in the previous figures.

and insertion of this muscle in *Glossotherium*. This suggests that the *M.p.m.* was more tendinous in *Glossotherium* than in tree sloths.

## DISCUSSION

Diverse characters of cranial osteology, dental structure, occlusal pattern, and reconstruction of masticatory musculature permit analysis of cranial function in *Glossotherium*. Interpretation of the significance of the structural–functional relationship makes it possible to distinguish primitive and derived characters by showing the relationship of different individual character states and character complexes to one another. Biomechanical principles shape the selection pressures upon these characters and, therefore, must be considered in an evolutionary analysis. Analysis of these characters and character complexes thus clarifies the evolutionary history and relationships of *Glossotherium* among the mylodonts and other sloth lineages. Characters examined in *Glossotherium* include those of previously determined functional significance that have been studied in other sloths (Naples, 1982, 1985a, 1986, 1987).

### Premaxilla and Predental Spout

All sloths possess a reduced premaxilla when compared to other mammals. It is non-tooth bearing, unfused, or sometimes only partially fused to the maxilla. It has lost bony contact with the nasals, and sometimes the left and right premaxillae do not contact one another (Owen, 1842; Parker, 1885; Winge, 1941; Romer, 1966; Naples, 1982). Premaxillae may be small and arrowhead-shaped (*Bradypus*); larger, broader, and triangular (*Choloepus*); or may form a pair of slender, poorly fused elongate rods (*Nothrotheriops*). The triangular premaxilla in *Glossotherium* is more elongate than in *Choloepus*, with left and right elements fused midventrally as well as to the maxilla, and lacks the large single foramen emarginating the anterior maxillary border. In addition to being longer, the premaxilla in *Glossotherium* is wider than in *Choloepus*.

The predental spout in *Glossotherium* is broad, slightly flared, and fused in a thick and deep mental symphysis (Fig. 1). The predental spout and premaxilla lengthen the anterior facial region in *Glossotherium*. Although a bony nasal septum is lacking, the large, rough-edged, trapezoid-shaped nasal opening provides attachment for extensive nasal cartilages and other soft tissues, allowing the presence of a thick flexible upper lip to aid food manipulation, as in *Choloepus* (Naples, 1982). The predental spout occurs in all sloth lineages and therefore is considered primitive in *Glossotherium*, although distal spout breadth is a derived character appearing in later mylodont sloths. Because earlier cranial reconstructions omitted a large amount of nasal tissue anteriorly, the face in *Glossotherium* has previously been reconstructed as too short and blunt (Owen, 1842; Stock, 1925; Fig. 6).

### Relationship Between the Zygomatic Arch, Postorbital Process, and Cranial Ligaments

The typical sloth zygomatic arch consists of a jugal bone with upper and lower processes and an elongate temporal squamosal process. In small ground sloths and tree sloths, the anterior and posterior zygomatic arch portions are unfused (Ameghino, 1889; Anthony, 1918; Stock, 1925; Romer, 1966; Webb, 1985). In the moderate-sized *Nothrotheriops*, the two portions meet but do not fuse, and in large sloths the arch is fused anteroposteriorly. Primitive ground sloths were small and had unfused zygomatic arches (Stock, 1925; Winge, 1941). This condition was probably retained from more insectivorous antecedents which had a reduced and divided zygomatic arch (Naples, 1985a) similar to Recent anteaters (Flower, 1882; Romer, 1966; Wetzel, 1985). Therefore, the fused jugal and squamosal process in *Glossotherium* (and a few other sloths) is a derived character and is probably necessary, in a biomechanical sense, to withstand large bending forces at the maxillo-jugal suture (Alexander, 1968; Currey, 1984).

Although all sloth jugals have at least two processes for attachment of the ligaments that complete the zygomatic arch, their orientations differ; horizontal (*Choloepus* and *Scelidotherium*) or vertical and above the posterior zygomatic arch attachment (*Eremotherium*). Other genera have upper processes ranging from nearly vertical (*Bradypus*) to only slightly above the squamosal process attachment (*Glossotherium*). The postorbital and upper jugal processes determine size, thickness, and orientation of the postorbital ligament. In *Choloepus*, the postorbital process is pointed with a small protuberance for postorbital ligament attachment. In other sloths the postorbital process is an elongate ridge (*Bradypus*). The jugal attachment in *Choloepus* is broad, resulting in an approximately triangular ligament, whereas that in *Bradypus* and *Nothrotheriops* is more rectangular. The posteriorly oriented upper jugal process in *Choloepus* and *Scelidotherium* minimizes the size of the jugal-temporal portion of the zygomatic arch ligament, whereas the more vertically oriented upper jugal process in *Bradypus* and *Nothrotheriops* maximizes ligament size and simultaneously covers more of the temporal fossa. In *Glossotherium*, the postorbital process is a long, rounded ridge, inflated by the frontal sinus. The expanded frontal bone maximizes the attachment area for the postorbital ligament posteriorly, shortening the distance to the attachment on the upper jugal process. The large sinus underlying the frontal bone is buttressed by bony ridges that divide the sinus into a series of rounded openings, somewhat like a honeycomb. These reinforcing ridges function as a series of I-beams, allowing the bone to withstand the greater multidirectional tensile stresses transmitted by the large, broad postorbital ligament (Alexander, 1968; Currey, 1984).

## Implications of CMJ Structure

The shape, orientation, and distance of the CMJ above the tooth row varies greatly among mammals and is directly correlative with diet. Typically, herbivores have shallow glenoid fossae that permit greater anteroposterior and labiolingual freedom of mandibular movement (Greaves, 1980). The glenoid fossa of *Glossotherium* and other fossil and Recent sloths exhibits this typical herbivore structure (Naples, 1982, 1987), even though other osteological structures may restrict condylar movement in one or more planes.

Several mechanisms for controlling the amount of freedom of mandibular movement have been described: (1) In *Choloepus*, a bony shelf forms an expansion of the lateral glenoid fossa that contacts the lateral projection of the mandibular condyle. When these surfaces meet during mastication, further anteromedial movement is prevented (Naples, 1982, 1985a). (2) *Bradypus* lacks a bony stop mechanism; condyle position control is maintained by the posterodorsally oriented lateral pterygoid muscles (Naples, 1985a). (3) In *Nothrotheriops*, lateral movement is restricted by a ridge on the ventral temporal squamosal process; medial movement is limited by a curved temporal surface, buttressed by thickening of the temporal-pterygoid suture (Naples, 1987).

Mandibular movement in *Glossotherium* is restricted medially by a bony stop that consists of a sharply defined depression on the lateral surface of the pterygoid bone that apposes the medial condylar occlusal facet. Although the bony stop in *Glossotherium* is medial rather than lateral (as in *Choloepus*), anterior and medial mandibular movements are similarly confined. Restriction of anterior and medial mandibular movement is important, because these genera possess caniniform teeth that require precise dorsoventral alignment during occlusion. This condition precludes the elevation of the CMJ which occurs in *Bradypus* and *Nothrotheriops*, genera that do not possess caniniform teeth.

These occlusal requirements correlate with the location of the CMJ, in approximately the same plane as the cheek tooth row in *Glossotherium*, a relationship that minimizes anteroposterior movement as the teeth occlude. A precise occlusal relationship between upper and lower caniniform teeth is of particular importance to *Choloepus*, a sloth with long caniniform teeth. It is also significant to *Glossotherium* because proper alignment of dental wear surfaces on the short caniniform teeth is required for biting. However, because the caniniform teeth are relatively short it is unnecessary for *Glossotherium* to gape as widely as *Choloepus*. At 45 degrees of gape the mandibular condyle in *Glossotherium* dislocates. This gape angle is 15 degrees less than the maximum gape predicted for *Choloepus*. The short anterior teeth in *Glossotherium* require an equivalent distance to clear as do those of *Bradypus* (another sloth with short anterior teeth), in addition to a greatly elevated CMJ and much anteroposterior mandibular movement during occlusion.

## Occiput and Occipital Condyles

Thickened parasagittal and lambdoidal crests surmount a large buttressed parietal-occipital sinus in

*Glossotherium.* The sinus is incompletely divided from the more anterior frontal-parietal sinus. Together, these partitioned sinuses elevate and reinforce the skull table anterodorsal to the braincase (Stock, 1925), increasing surface area for attachment of the postorbital ligament and temporal musculature laterally, and the *M. splenius capitus, M. trapezius,* and other deep neck and back muscles posteriorly.

The occipital condyles are sharply convex and posteroinferiorly oriented, indicating that the head of *Glossotherium* was carried slightly higher than has been described or illustrated previously (Owen, 1942; Stock, 1925). The occipital condyles are broad and widely spaced. This arrangement would restrict horizontal cranial movements if the head were short; however, the long relatively narrow skull in *Glossotherium* compensates for restricted mobility of the head on the neck at the occiput, while requiring a strong bony support platform and neck muscles with a large mechanical advantage upon which to pivot the skull. Extension of cranial sinuses into the occipital area is not seen in tree sloths or in other fossil sloths (Owen, 1842; Allen, 1913; Stock, 1925; Naples, 1982, 1985a, 1987). Expansion of the cranial sinuses into the parietal area increases the surface area for the attachment of neck muscles including the *M. trapezius, M. splenius capitus, M. semispinalis capitus,* and *M. longissimus capitus.* These muscles, in conjunction with muscles of the occipital triangle and other intrinsic back muscles, move and maintain posture of the head and neck in mammals.

The head of *Glossotherium* is relatively larger and more robust than that of *Nothrotheriops* and the tree sloths and, therefore, requires relatively larger muscles (and other structural modifications in the occipital region) to control head movement and posture. Movement of the head from side to side, a motion useful in browsing or grazing, is enhanced in *Glossotherium* by a triangular gap between the transverse processes of the atlas and axis (cervical vertebrae 1 and 2). This gap is created by the posterolateral orientation of the transverse process of the axis. The triangular-shaped gap receives the transverse process of the atlas, permitting *Glossotherium* a wider range of head movement than would be possible otherwise. This osteological and muscular arrangement is different from other sloths studied here, and therefore can be considered a derived condition (Alexander, 1968).

### Pterygoid Region

In *Glossotherium,* the elongate pterygoid bones are similar in profile to *Nothrotheriops,* with the greatest elongation anteriorly; however, *Glossotherium* lacks the inflated pterygoid sinuses seen in *Nothrotheriops* and *Choloepus.* As in *Bradypus,* the elongated pterygoid flanges are thin-walled in *Glossotherium* and buttressed laterally by ridges marking the origins of the medial and lateral pterygoid muscles.

### Dental Wear Striations

Wear striations on the teeth of *Glossotherium* trend along the anterolingual–posterolabial axis. The transitions from hard to soft dentine are smooth and flush lingually, and stepped labially (Greaves, 1973; Rensberger, 1973; Costa and Greaves, 1981). These striations indicate that this genus has an anteromedially directed power stroke common to other mammals (Hiiemae, 1978). The amount of anteroposterior movement in *Glossotherium* is somewhat less than that observed in *Bradypus* or *Nothrotheriops.*

### Masticatory Musculature

The muscles of mastication in *Glossotherium* conform to the general plan observed in other sloths with respect to muscle division, probable fiber architecture and bony attachments. The most anterior segment of the superficial masseter (*M.m.s.*—5) restricts the gape in *Glossotherium* to 22 degrees, a derived condition (Table 3). Manipulation of skulls and mandibles indicates that gape would not be restricted by joint structure until at least 45 degrees. Superficial masseter length in *Glossotherium* is shorter than in other sloths because the insertion on the mandibular angle projects less far posteriorly. However, the overall insertion area is probably comparable because the angular process is deeper dorsoventrally than in other sloths. Resolution of the forces generated by superficial masseter segments results in a line of action oriented approximately halfway between the lines of action of the same muscle segments in the tree sloths, and illustrates a retention of the primitive muscle orientations in the tree sloths and *Glossotherium* (Table 4). The short deep insertion of the superficial masseter makes the range of muscle segment orientation greater in *Glossotherium* than in other sloths and may enhance mandibular movement patterns in this genus, particularly in the vertical plane (Fig. 7).

The deep masseter (*M.m.p.*) in *Glossotherium* is relatively larger than in the tree sloth *Choloepus,* but similar in relative size to its homologues in *Bradypus* and *Nothrotheriops.* Of these four sloths, only *Choloepus* retains the primitive small relative mass, the distance from origin to insertion, and the line of action for the deep masseter. In megatheriids and *Glossotherium,* the deep masseter is relatively larger than in *Choloepus.* This muscle is anterodorsally oriented in *Bradypus* and *Glossotherium,* although the origin is mostly from the relatively wider descending jugal process in *Glossotherium,* emphasizing the anterior component of the line of action (Table 4).

The temporalis (*M.t.*) in *Glossotherium* has a more elongate origin than in other sloths and a resolved

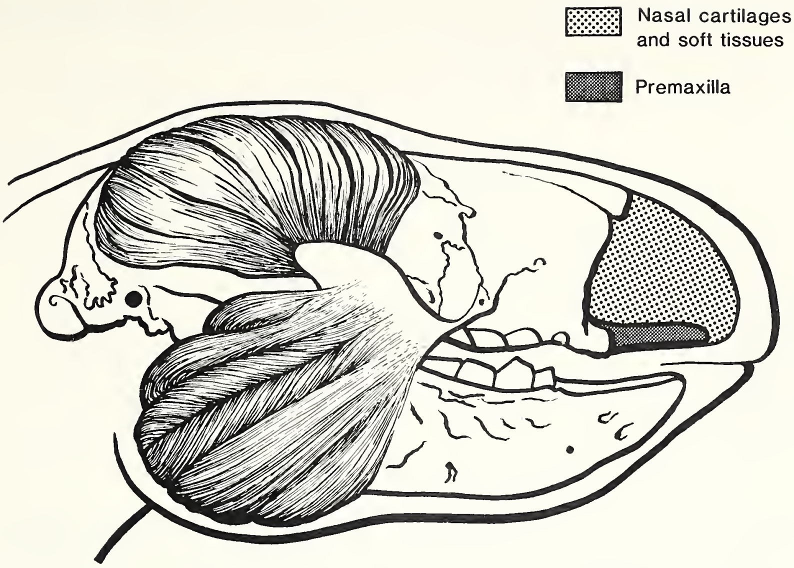

**Figure 7.** Restoration of the masticatory musculature, ligaments, and nasal cartilages in *Glossotherium.* The proposed outline of facial shape is longer than has been previously predicted due to restoration here of large nasal cartilages and other soft tissues supporting a thick and (probably) flexible upper lip. These anterior tissues were restored in proportion to those seen in radiographs of live tree sloths.

line of action between the lines of action of this muscle in the tree sloths. The temporalis in *Glossotherium* is relatively larger than in tree sloths and *Nothrotheriops* and could have produced greater forces in mandibular elevation, while retaining primitive muscle orientation.

The zygomaticomandibularis (*M.z.*) in *Glossotherium* is relatively as large as those in *Bradypus* and *Nothrotheriops* and relatively larger than that of *Choloepus. Choloepus* lacks an ascending jugal process, and therefore has retained the primitive condition of a relatively small, horizontal origin for the *M.z.* In *Glossotherium,* the *M.z.* originates from an expanded, posterodorsally oriented ascending process and emphasizes the anterior component of the line of action more than in other sloths. This is a derived condition (Table 4).

Although relatively larger, the superior lateral pterygoid head in *Glossotherium* is typical of that in other mammals and *Choloepus* with regard to origin and insertion. The anterodorsal orientation of the lateral pterygoid in *Glossotherium* and *Choloepus* reflect the primitive condition in contrast to the posterodorsally oriented lateral pterygoids in megatheriids. The inferior lateral pterygoid head in *Glossotherium* converges slightly toward the superior lateral pterygoid head at its insertion, which is in contrast to the condition found in *Choloepus.* For both sloths, the anteroposterior alignment of the anterior teeth is critical; in addition, the mandibular condyles are wider mediolaterally and not freely movable anteroposteriorly as they are in *Bradypus* and *Nothrotheriops.* The two lateral pterygoid heads converge strongly in *Bradypus* and *Nothrotheriops,* perhaps to permit them to act in concert across a smaller area, giving the mandibular condyle greater anteroposterior freedom of movement. Minor convergence of the lateral pterygoid heads in *Glossotherium* decreases mechanical advantage slightly; however, the broad condyle in *Glossotherium* may compensate for this. Close apposition of the insertion of the lateral pterygoid heads in *Glossotherium* may refine the mediolateral mandibular movements important for chewing with the molariform teeth and biting with the anterior teeth.

The medial pterygoid in *Glossotherium* is more vertical and anterodorsal than in *Choloepus* and *Bradypus,* reflecting a derived orientation (Table 4). This muscle is relatively larger than in tree sloths or *Nothrotheriops* and may be important in controlling the position of the mandibular angle during elevation in order to occlude the short caniniform teeth properly. Such muscular control may act as an occlusal guide mechanism to allow proper wear surface apposition, rather than the size and shape of the caniniform teeth (Scapino, 1972).

## ESTIMATION OF GAPE

The degree to which sloths can gape is one factor that may limit the manner in which they feed. The ability to open the mandible to a given degree is determined by several factors, which include (1) mandibular length and shape; (2) position, orientation, and structure of the CMJ; and (3) shape, length, and orientation of the masticatory muscle segments. From skull and jaw manipulations, it is

**Table 4. The angle in degrees of the orientation of the masticatory muscles in four sloth genera compared in this study. The angles were measured as the number of degrees of divergence from the occlusal plane in each specimen (N = 5 of each genus). Zero degrees is toward the anterior of the cranium at the plane of the cheek tooth row. The numbers in italics denote derived muscle orientations.**

| | **Masticatory muscle orientation** | | | |
|---|---|---|---|---|
| | **Sloth lineages** | | | |
| | **Mylodontid** | **Megatheriid** | | **Megalonychid** |
| | ***Glossotherium*** | ***Nothrotheriops*** | ***Bradypus*** | ***Choloepus*** |
| Masticatory muscle | | | | |
| *M. masseter superficialis* | 325° | ***349°*** | 318° | 323° |
| *M. masseter profundus* | ***20°*** | ***111°*** | ***48°*** | ***123°*** |
| *M. temporalis* | 125 | ***112°*** | ***118°*** | 141° |
| *M. zygomaticomandibularis* | 57 ° | 83° | 90° | 79° |
| *M. pterygoideus lateralis* | 12° | ***130°*** | ***125°*** | 20° |
| *M. pterygoideus medius* | ***300°*** | 330° | 330° | 318° |

clear that osteologic restrictions on gape are not limiting up to 45 degrees. At greater gape than 45 degrees, the mandibular condyle dislocates and the mandibular angle impinges upon the paroccipital process. In addition, gape is limited by the degree to which masticatory muscles can be stretched without damage, about twice the resting length (Carlsöö, 1942).

The distance to which masticatory muscle segments in *Glossotherium* would be stretched at gapes of 20, 25, 30, 35, 40, and 45 degrees suggests that *M.m.s.*—5 could stretch no more than 22 degrees without damage (Table 3). No other superficial masseter segments restrict mandibular opening to less than 45 degrees, although three other muscles (the *M. temporalis, M. zygomaticomandibularis,* and *M. pterygoideus medius*) would have been overstretched. The Recent tree sloth *Choloepus* can gape to approximately 60 degrees; the larger distance is important in an animal with elongate caniniform teeth. In the other Recent tree sloth, *Bradypus,* the maximum gape is approximately 40 degrees (Naples, 1985a). Similarly, this method predicts a 25-degree gape in *Nothrotheriops,* a sloth with a more elongate skull and mandible and no anterior teeth (Naples, 1987).

In *Glossotherium,* the anteroventral segment of the superficial masseter limits maximum gape to less than 23 degrees, although no other muscle or segment is limiting until almost 35 degrees. In all sloths studied to date, gape is limited by *M.m.s.*—5, whether other muscles or segments constrain mandibular opening more than do bones and joints. The variable presence of short caniniform teeth in this sloth indicates that caniniform tooth length, rather than presence or absence, is the most important factor in setting maximum gape requirements. Even though the maximum degree of mandibular rotation in *Glossotherium* was small, the buccal opening was large, because of the large skull, long maxillae, premaxillae supporting a thick upper lip, long mandible, and broad predental spout. The large buccal opening in *Glossotherium* was important for ingestion of the bulky leafy vegetation preferred by these sloths (Stock, 1925).

## DETERMINATION OF DERIVED CHARACTERS AND IDENTIFICATION OF CHARACTER COMPLEXES IN *GLOSSOTHERIUM*

Cranial characters in *Glossotherium* were compared to the distribution and state of those characters among other sloth lineages. Refinement of our understanding of xenarthran relationships relies upon the ability to test hypotheses concerning "the distribution of characters that can be assumed to be uniquely derived within the group (Engelmann, 1985)." Therefore, identification of derived characters and their interrelationships, by studying biomechanical constraints upon them, can provide important information regarding sloth relationships and evolutionary history.

Previous studies identifying sloth cranial characters generally agree (Patterson and Pascual, 1972; Engelmann, 1985; Webb, 1985; Naples, 1982, 1985a, 1987), based upon comparison with the earliest mylodont sloths and other mammals, that the following eight cranial characters are primitive for sloths: (1) a large diastema, (2) a CMJ at the level of the cheek tooth row, (3) elongate caniniform anterior teeth, (4) a large gape, (5) a basicranial angle approaching zero degrees, (6) an incomplete zygomatic arch, (7) a long facial region, and (8) bilobate teeth. The present study has identified 24 additional cranial characters, both primitive and derived, based upon their relationships with the eight characters listed above (Table 5).

In all animals, morphology is determined, in part, by biomechanical constraints delimiting the function of critical aspects of character associations. Identification of interrelated characters is important because treating a character complex as a unit reduces the likelihood that biases will be introduced

**Table 5. The distribution and state of cranial characters in four genera of sloths, representing all three sloth lineages. Characters in italics are derived.**

| Cranial character | *Glossotherium* | *Nothrotheriops* | *Bradypus* | *Choloepus* |
|---|---|---|---|---|
| Dental formula | $\frac{5}{4}$ or $\frac{4}{3}$ | $\frac{4}{3}$ | $\frac{5}{4}$ | $\frac{5}{4}$ |
| Anterior tooth length | *Short* | *None* | *Short* | Elongate |
| Anterior tooth shape | Caniniform | | Chisel-shaped | Caniniform |
| Upper cheek teeth | Lobate; anterior–posterior > labio-lingual axes; $M^1$–$M^4 \cong$ size | *Subrectangular;* labio-lingual > anterior–posterior axes; $M^1$, $M^4 < M^2$, $M^3$ | *Ovoid;* labio-lingual $\cong$ anterior–posterior axes; $M^1$–$M^4 \cong$ size | *Ovoid;* anterior–posterior > labio-lingual axes; $M^1$, $M^4 < M^2$, $M^3$ |
| Lower cheek teeth | Lobate; anterior–posterior > labio-lingual axes; $M_1 \cong M_2 < M_3$ | *Ovoid;* labio-lingual > anterior–posterior axes; $M_1 < M_2 < M_3$ | *Ovoid, subrectangular;* anterior–posterior $\cong$ labio-lingual axes; $M_1 \cong M_2 < M_3$ | *Ovoid;* anterior–posterior > labio-lingual axes; $M_1 \cong M_2 \cong M_3$ |
| Premaxilla | Large, arrowhead | *Elongated, slender,* unfused | Arrowhead | Arrowhead |
| Nasal | Elongate | Elongate | *Extremely short* | *Short* |
| Maxilla | Flares widely | *Narrow* | Flares widely | Flares slightly |
| Tooth row shape | Wider anteriorly | *Parallel* | Wider anteriorly | Wider anteriorly |
| Postorbital process | Small, rounded | Small, rounded | *Large, rounded* | *Large, pointed* |
| Location of coronal suture | ⅔ toward rear | ⅔ toward rear | *½ toward rear* | ⅔ toward rear |
| Zygomatic arch | *Complete* | *Complete* | Open | Open |
| Ascending process | *Yes* | *Yes* | *Yes* | No |
| Angle from cheek tooth row | 30° | 60° | *55°* | — |
| Descending process | *Yes* | *Yes* | *Yes* | *Yes* |
| Angle from cheek tooth row | 70° | 40° | 45° | 60° |
| Height of CMJ | Equals tooth row level | *Above tooth row* | *Above tooth row* | Equals tooth row level |
| Condyle shape | Labio-lingual axis wider | *Anterior–posterior axis longer* | *Anterior–posterior axis longer* | Labio-lingual axis wider |
| Bony stop present | *Yes; medial* | None | None | *Yes; lateral* |
| Degrees gape | *22°* | *25°* | *40°* | 60° |

into a phylogenetic analysis from inadvertent overrepresentation of a single complex. Some of these interrelationships, and the most important aspect of the character or character states involved, have been revealed in *Glossotherium* by the present study (Table 6). Twelve derived characters from Table 5 have been grouped into complexes according to interdependence of function (Table 6). For each of the four complexes identified, the state of one character determines the morphology of those associated with it, and whenever one of these derived characters is present, the others must be also to enable the complex to function.

In Complex I, the shortness of the caniniform teeth is critical because short caniniforms reduce the need for a wide gape or a long diastema between molariform and caniniform teeth. Because a wide gape is not necessary to clear the anterior teeth for

**Table 6. Derived cranial characters forming functional complexes in *Glossotherium*. For each complex the character listed first is acted upon most strongly by biomechanical constraints, which determine the state of others in the complex.**

Complex I

1. Short caniniform teeth
2. Lack of a diastema between caniniform and molariform teeth
3. Reduced distance for gape

Complex II

1. Caniniform teeth (sometimes) present
2. Differentiated facets on mandibular condyle (wider labiolingually); forms a bony stop mechanism
3. Concave glenoid fossa with a facet for the bony stop

Complex III

1. Increased mechanical advantage of superficial masseter and medial pterygoid muscles
2. Angular process of mandible deepened posteroventrally
3. Pterygoid flange elongated posteroventrally

Complex IV

1. Increased mechanical advantage of the *M. zygomaticomandibularis;* line of action more vertical and anteriorly oriented
2. Posteriorly oriented ascending jugal process
3. Increased area for origin of the *M. zygomaticomandibularis* by reduction of the size of the condylar notch

biting, *Glossotherium* can retain the primitive state of the CMJ (in the same plane as the cheek tooth row). Likewise, a long diastema which would increase the distance between the anterior teeth and the joint to maximize the clearance distance of the caniniform teeth at a given degree of mandibular rotation is unnecessary. The resulting (relatively short) mandible in *Glossotherium* also permits the muscles of mastication to have a greater mechanical advantage.

In Complex II, the presence of caniniform teeth (even if only in some specimens), which require precise alignment for proper function, is critical. A CMJ at the same level as the cheek tooth row minimizes the anteroposterior tooth movement during occlusion. Although retention of a low CMJ is primitive, the bony stop developed on the mandibular condyle (preventing excess mediolateral mandibular movement) is derived.

The limiting character in Complex III is the maximization of mechanical advantage of the *M. pterygoideus medius* and the *M. masseter superficialis,* which is achieved in *Glossotherium* by retaining the primitive muscle orientation seen in animals with elongate anterior biting teeth (Turnbull, 1970; Herring and Herring, 1974; Weijs, 1980; Lucas, 1981; Greaves, 1983). Optimization of the mechanical advantage of these jaw closing muscles is important because they generate much of the force that produces the pattern of mandibular movement during the masticatory power stroke. In animals with elongate anterior teeth, maximum force is needed at the time of intercuspation of the tooth tips to grip and pierce any objects bitten (Herring and Herring, 1974; Weijs, 1980; Lucas, 1981; Greaves, 1983). In contrast, the caniniform teeth in *Glossotherium* are blunt and were probably used for crushing thick plant stems and gripping bulky clumps of leaves. Whereas the maximum force needed in animals with pointed anterior teeth is after intercuspation, when the jaw is almost closed (10 to 0 degrees; Weijs, 1980), in *Glossotherium* maximum force would be needed from prior to intercuspation to the beginning of intercuspation (when the jaw is open from 22 to 5 degrees). In contrast to the condition in the other animals, the origins of the *M.p.m.* and the *M.m.s.* in *Glossotherium* are from an elongated pterygoid flange and a descending jugal process, and the insertions are on the lingual and labial sides of a posteroventrally elongated angular process. Ventral displacement of these muscles shifts the arc of maximum muscle effectiveness to the larger gapes (22 to 10 degrees) in *Glossotherium* without sacrificing either the distance to which the sloth could gape or the amount of force the muscles could generate.

In Complex IV, maximization of mechanical advantage in the *M. zygomaticomandibularis* is critical and results in the posterior orientation of the ascending jugal process and decreased size of the mandibular notch. The *M.z.* in *Glossotherium* is largely responsible for horizontal translation of the mandible (an important action in the latter portion of the masticatory stroke) as well as some elevation. Optimization of the mechanical advantage and mass of this muscle is important because ventral displacement of the *M.p.m.* and *M.m.s.* (described in Complex III) reorients the lines of action of those muscles to be less effective in mandibular translation.

## CRANIAL MORPHOLOGY AND DIET *IN GLOSSOTHERIUM*

Stock (1925, 1930) suggested that *Glossotherium* was primarily a grazer, based upon tooth structure he determined to be of a "grinding" type. *Glossotherium* is the most common of the three sloth genera preserved in the Rancho La Brea asphalt deposits; *Nothrotheriops* is less common and *Megalonyx* Jefferson, 1799, is quite rare. The diet of *Nothrotheriops* is well documented through the analysis of dung contents in Rampart Cave, New Mexico (Hansen, 1978). Analyses of cranial structure and dental occlusion patterns (Naples, 1987) agree well with Hansen's (1978) results, suggesting that morphological analyses predict food habits accurately for sloths. Details of the diet of *Glossotherium* are unknown; no dung deposits are available for analysis, therefore dietary preferences must be deduced from sloth morphology.

In comparison to the teeth of *Nothrotheriops* and the tree sloths, which are all considered browsers, the cheek teeth in *Glossotherium* are relatively larger, have more complicated shapes, and retain a layer of cementum surrounding all sides. Analyses of wear striation orientation and flush or stepped transitions between hard and soft dentine (Greaves, 1973; Rensberger, 1973) has demonstrated that *Glossotherium* had an anteromedially directed masticatory power stroke. The path of mandibular movement is arcuate, with more medial translation than anterior movement (Fig. 2B). Emphasis on the medial component of motion ensures maximum shearing efficiency because this movement pattern brings the obliquely oriented cheek tooth cutting edges into contact perpendicular to their widest axes. The widest axes of the cheek teeth become less oblique posteriorly along the tooth row. This correlates with a change in the path of mandibular movement from anterior to posterior, with the greatest component of motion present at $C_1$ and the least at $M_3$.

Other evidence suggesting that the environment near Rancho La Brea was partially open scrub and grassland is the relative abundance of herbivores that both browse and graze. For example, camels, horses, antilocaprids, and bison were among the most common animals preserved. Conversely, the more strictly browsing forms, such as deer, are rare, as is the browsing sloth, *Nothrotheriops*. A mixed-forest, scrub, and grassland setting is also supported by the presence of both mastodons and mammoths. The former were browsers whereas the latter were grazers (Stock, 1930; Shaw and Quinn, 1986; Akersten *et al.*, 1988).

Although more suited to grazing than the other sloths in the La Brea region, on the basis of dental evidence, *Glossotherium* was probably less efficient at ingesting grasses than some of the other local grazers (Janis, 1976). In comparison to horses, camels, antilocaprids, and bisons, which have high-crowned, ever-growing teeth, and mammoths, which have continually replaced teeth, the sloth dental apparatus, with intermittent shearing surfaces acting alone, would have been too inefficient at reducing plant materials to small particle size to permit the sloths to obtain sufficient nutritive value from the food (Hansen, 1978). However, with a low projected metabolic rate, leading to a reduced energy requirement per unit body weight (Almeida and Fialho, 1924; Britton, 1941; McNab, 1978) a large body size, and an unusually capacious gut with a probable foregut fermentation site, *Glossotherium* could probably survive better on foods of lower nutritional value than could other sloths and browsing herbivores in the area. Observations on Recent tree sloths show that they have an unusually slow rate of passage of ingesta through the gut (Jeuniaux, 1962; Denis *et al.*, 1967; Moir, 1968; Goffart, 1971; Bauchop, 1978; Parra, 1978). It is reasonable to assume that *Glossotherium* also had a slow rate of passage of food through the digestive tract. This might have enabled these sloths to obtain sufficient nutrition from high fiber foods to compete effectively for resources with the other La Brea herbivores. Although it is likely that grasses were more important in the diet of *Glossotherium* than in *Nothrotheriops*, the former probably ate a variety of foliage plants as well, and would probably be better considered a browser–grazer than a "pure" grazing form.

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# Contributions in Science

## *Carnotaurus sastrei* Bonaparte, the Horned, Lightly Built Carnosaur from the Middle Cretaceous of Patagonia

J. F. Bonaparte, F. E. Novas, and R. A. Coria

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# *CARNOTAURUS SASTREI* BONAPARTE, THE HORNED, LIGHTLY BUILT CARNOSAUR FROM THE MIDDLE CRETACEOUS OF PATAGONIA

J. F. BONAPARTE, F. E. NOVAS, AND R. A. CORIA[1]

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[1] Sección Paleontologia de Vertebrados, Museo Argentino de Ciencias Naturales, "Bernadino Rivadavia," Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina.

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**ABSTRACT.** *Carnotaurus sastrei* Bonaparte, 1985, is known from Cretaceous deposits referred to the Gorro Frigio Formation (Albian or Cenomanian) of Chubut Province, Patagonia, Argentina. It is an unusual theropod, with two short, stout frontal horns; a very weak contact between dentary and postdentary bones; cervical vertebrae quite derived, with small neural spines and very pronounced epipophyses; forelimbs extremely reduced; and long, slender hindlimbs. *Carnotaurus sastrei* shares several derived and primitive characters with *Abelisaurus comahuensis* Bonaparte and Novas, 1985, from the Allen Formation, Maastrichtian of Patagonia, Argentina: maxilla short and high in its anterior half, a small maxillary fenestra, nasals strongly decorated, wide contact between postorbital and lachrymal above the orbit, elongate quadrate, and ventral branch of the squamosal ventrally directed. These features suggest that both species belong to the same family, Abelisauridae Bonaparte and Novas, 1985.

The Noasauridae, represented by *Noasaurus leali* Bonaparte and Powell, 1980, from the Lecho Formation, Maastrichtian, northwestern Argentina, appears to be related to the Abelisauridae because the contained species have a similar type of cervical vertebrae, *i.e.*, with reduced neural spines and well-developed, spine-like epipophyses. Comparative analyses suggest that Abelisauridae and Noasauridae share more characters with Ceratosauridae than with any other Theropoda. Two superfamilies are recognized: Ceratosauroidea (including Ceratosauridae, Abelisauridae, and Noasauridae) and Tyrannosauroidea (including Allosauridae and Tyrannosauridae).

**RESUMEN.** *Carnotaurus sastrei* Bonaparte, 1985, proveniente de depósitos Cretacicos referidos a la Formación Gorro Frigio (Albiano o Cenomaniano) de la Provincia del Chubut, Patagonia, Argentina, es un inusual terópodo con dos cortos y robustos cuernos frontales; mandíbula con débil contacto entre los elementos dentarios y postdentarios; vértebras cervicales especializadas, con espinas neurales pequeñas y epipófisis muy pronunciadas; miembros anteriores sumamente reducidos; y miembros posteriores largos y gráciles. *Carnotaurus sastrei* comparte una serie de caracteres derivados y primitivos con *Abelisaurus comahuensis* Bonaparte y Novas, 1985, de la Formación Allen, Maastrichtiano de Patagonia, Argentina: maxilar corto y alto en su sector anterior, fenestra maxilar pequeña, nasales fuertemente decorados, postorbital y lacrimal con amplio contacto por encima de la órbita, cuadrado largo, y escamoso con rama ventral dirigida ventralmente. Estos caracteres sugieren que ambos taxones pertenecen a la familia Abelisauridae Bonaparte y Novas, 1985.

La familia Noasauridae, representada por *Noasaurus leali* Bonaparte y Powell, 1980, de la Formación Lecho, Maastrichtiano, NW de la Argentina, parece estar relacionado a la familia Abelisauridae, debido a que presenta un tipo similar de vértebras cervicales, con espinas neurales reducidas y epipófisis desarrolladas. Las comparaciones efectuadas sugieren que Abelisauridae y Noasauridae comparten más caracteres con los Ceratosauridae que con otros terópodos conocidos. Se reconocen dos superfamilias: Ceratosauroidea (que incluye a Ceratosauridae, Abelisauridae, y Noasauridae) y Tyrannosauroidea (que incluye a Allosauridae y Tyrannosauridae).

## INTRODUCTION

During fieldwork of the 8th Paleontological Expedition to Patagonia, within the project "Jurassic and Cretaceous Terrestrial Vertebrates of South America" sponsored by the National Geographic Society, the skeleton of a theropod of rather great size was excavated. It was in a good state of preservation, with all of the preserved bones perfectly articulated. Skin impressions were found in the area of its right side, perhaps the first recorded among the carnosaur dinosaurs. However, weathering had affected the central and distal parts of the tail, most of the tibiae, both fibulae, and the hind feet. The remainder of the skeleton was complete, articulated, and with some lateromedial deformation that was more pronounced in the skull.

*Carnotaurus sastrei* was briefly described by Bonaparte (1985). It was noted that there are strong differences between it and the Cretaceous carnosaurs from the northern continents, especially in the skull, axial skeleton, and in the striking reduction of the forelimbs. Bonaparte and Novas (1985) recognized that *Abelisaurus comahuensis* represented a new family of the Carnosauria, Abelisauridae, to which *C. sastrei* was referred. This family is clearly defined by characters of the skull: large infratemporal fenestra; elongated quadrate; posteriorly directed squamosal with a ventral, rod-like process; and a small maxillary fenestra located very near the preorbital opening.

The marked anatomical differences of this family of Patagonian theropods, in comparison with theropods from the Northern Hemisphere, have been interpreted by Bonaparte (1985, 1986b) and Bonaparte and Novas (1985) to be the result of the long geographic separation of the Laurasian and Gondwanian supercontinents. According to the paleogeographic evidence (Bonaparte, 1986b), the isolation occurred from the late Middle Jurassic to the Late Cretaceous (Campanian).

The following abbreviations are used in this paper: AMNH, American Museum of Natural History; MACN-CH, Museo Argentino de Ciencias Naturales "B. Rivadavia," Colección Chubut; and USNM, United States National Museum of Natural History.

## SYSTEMATICS AND PALEONTOLOGY

### Order Saurischia Seeley, 1888
### Suborder Theropoda Marsh, 1881
### Infraorder Carnosauria Huene, 1920
### Family Abelisauridae Bonaparte and Novas, 1985

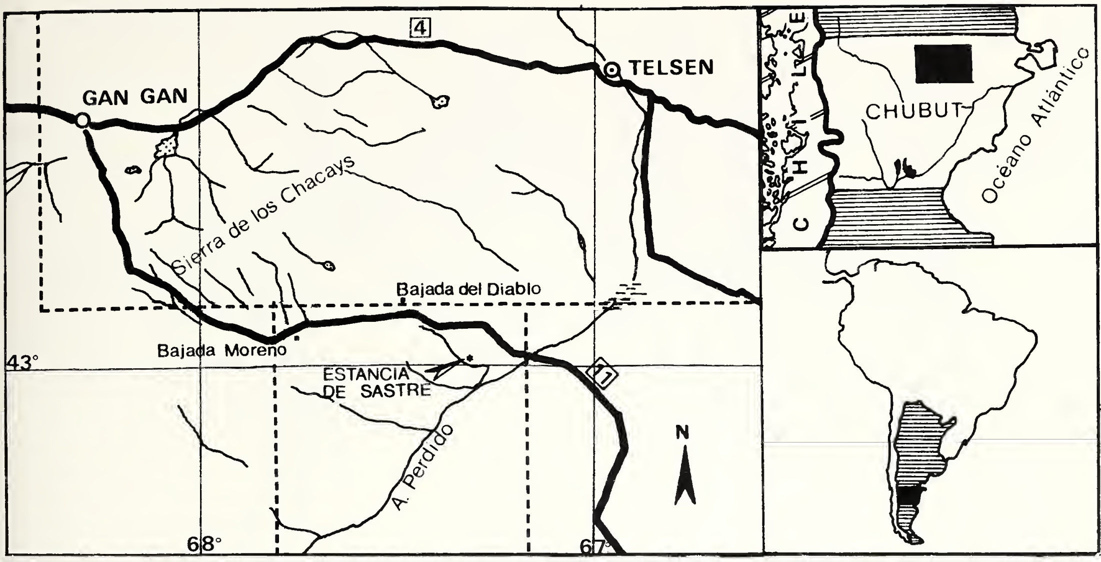

Figure 1. Map showing the locality where *Carnotaurus sastrei* was found.

## Genus *Carnotaurus* Bonaparte, 1985
## Type species *Carnotaurus sastrei* Bonaparte, 1985

**HOLOTYPE.** MACN-CH 894. Almost complete skeleton, with skin impressions, lacking medial and distal parts of the tail, central and distal parts of the tibiae, both fibulae, and hind feet.

**LOCALITY.** Estancia Pocho Sastre, near Bajada Moreno, Department of Telsen, Province of Chubut, Patagonia, Argentina (Fig. 1).

**HORIZON AND AGE.** Near the top of the Gorro Frigio Formation, Cretaceous (Albian or Cenomanian).

**REVISED GENERIC DIAGNOSIS.** Abelisaurid carnosaur, with skull shorter and higher than in *Abelisaurus* and other theropods, and with deep snout and prominent frontal horns. Orbits divided into two parts: an upper, rounded section anterolaterally projected for the eyes, with a pronounced posterodorsal orbital wall, and a lower, dorsoventrally elongated section. Supratemporal opening small, with parietal and squamosal forming a high posterior wall and having a low, lateral border. Infratemporal and preorbital openings smaller than in *Abelisaurus*. Quadrate very high, and squamosal having a short, rod-like ventral projection. Loose contact between dentary and postdentary bones, forming a large mandibular fenestra. Cervical vertebrae behind the axis with reduced neural spines and high, well-developed epipophyses. Sacrum with seven fused vertebrae. Forelimbs reduced, with extremely short and stout radius and ulna, both provided with large, convex distal ends. Ilia long and square-shaped. Pubes, ischia, and femora long and slender.

## CRANIAL SKELETON

### Skull

The skull of *Carnotaurus sastrei* (Figs. 2–5) was somewhat laterally compressed in fossilization, mainly around the temporal and orbital openings. It is short and high, with two robust frontal horns. Both the skull and lower jaws have loose sutures between some bones that suggest kinesis. Most of the lateral and dorsal surfaces of the skull have sharp rugosities, canals, and small foramina. But the occipital region, the quadratojugal, the supraoccipital region, and the occipital crest are smooth. These areas of the skull were covered by a muscular mass, whereas in the rugose areas the soft covering possibly was horny.

The *premaxilla* is thick and massive, with the narial opening in a high position. The posterodorsal process is not exposed. Below the external nares there is a wide depression of smooth bone, very different from the rest of the muzzle. It may have been the position of a salt gland comparable to that of some herbivorous dinosaurs (Osmolska, 1979).

The *maxilla* is very short and high, with one maxillary fenestra that is dorsoventrally elongated, anteroposteriorly short, and located very near the anterior border of the preorbital opening. The latter opening is also higher than long, quite different from the situation in tyrannosaurids (Fig. 7) and dromaeosaurids.

The *lachrymal* has only a small anterior projection that contacts the nasal (Fig. 2). The ventral projection is posteriorly convex, as in *Abelisaurus* (Bonaparte and Novas, 1985); fig. 7.

The *jugal* is very short and high, with the anterior projection dorsoventrally thick. The suture with

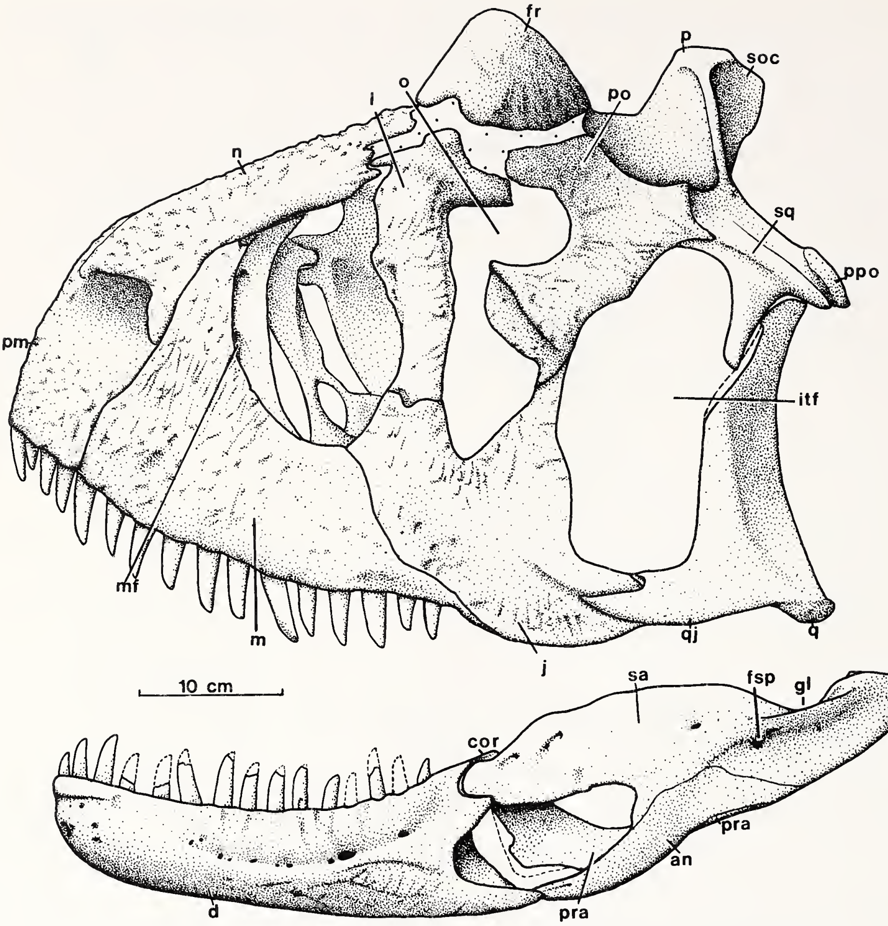

**Figure 2.** *Carnotaurus sastrei.* Skull and left lower jaw in lateral view. an, angular; ar, articular; cor, coronoid; d, dentary; fr, frontal; fsp, posterior surangular foramen; itf, infratemporal fenestra; j, jugal; l, lachrymal; mx, maxilla; mxf, maxillary fenestra; n, nasal; o, orbital opening; p, parietal; pmx, premaxilla; po, postorbital; ppo, paraoccipital process; pra, prearticular; q, quadrate; qj, quadratojugal; rt, retroarticular process; sa, surangular; soc, supraoccipital; sq, squamosal.

the maxilla is rigid, whereas those with the lachrymal, postorbital, and quadratojugal are weak, suggesting that kinesis was possible.

The *postorbital* is proportionally large, with a conspicuous anteroventral process that defines the lower rim of the orbit and closely approaches the lachrymal. The postorbital has a wide contact with the frontal horn. The sutures with the squamosal and the dorsal process of the jugal are weak, suggesting that movement was possible.

The *squamosal* is relatively small, with little participation of the supratemporal fenestra. The ventral projection is rod-like, with a short contact with the quadratojugal. The cavity for the quadrate head is not deep, and the posteroventral projection is modest.

The *quadrate* and *quadratojugal* are fused to one another and show a movable contact with the jugal. The quadrate is dorsoventrally long, with the lower condyles well defined in medial view and less so in lateral view. The anteromedial projection is high, and it is most easily distinguished at the contact with the quadrate branch of the pterygoid. In occipital view (Fig. 4) the quadrates are dorsoventrally long and wide, showing a rather sharp border running down from near the paraoccipital process, separating the posterolateral surface from the posteromedial one.

The *nasals* show more pronounced rugosities than do other parts of the skull. They are transversely convex and almost straight anteroposteriorly. The anteroventral process is pronounced. The sutures of the nasals with the frontals, the premaxillae, and lachrymals are weak, suggesting mobility. But the union of the nasals with the maxillae, although not fused, suggests that it was more rigid than those cited above.

The *frontals* are fused with the anterior part of the parietals, but the sutures with the lachrymals and postorbitals are loose. The horns of this species

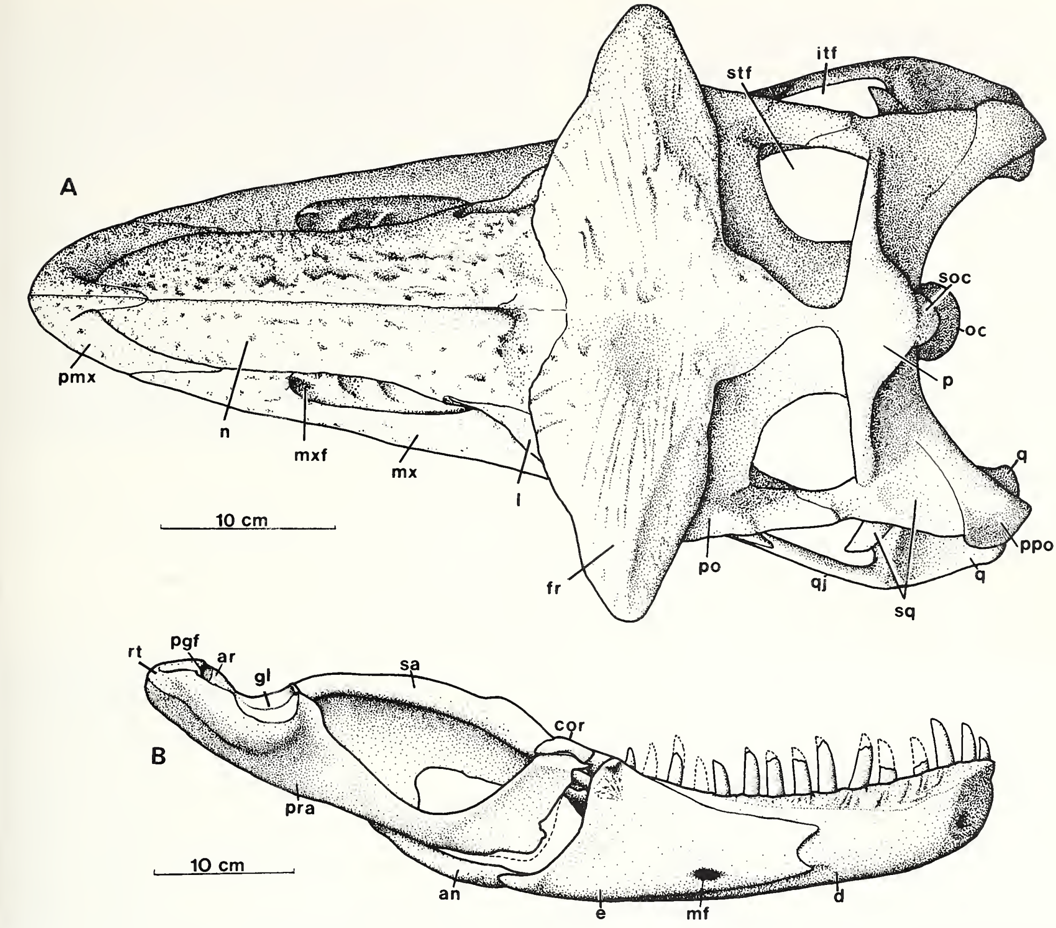

**Figure 3.** *Carnotaurus sastrei.* Skull (**A**) in dorsal view with lateral compression in premaxilla, maxilla, and quadratojugal, and displacement of the premaxilla corrected. Left lower jaw (**B**) in medial view. Abbreviations as in Figure 2, and: e, splenial; gl, glenoid; mf, Meckelian foramen; oc, occipital condyle; pgf, post-glenoid fossa; rt, retroarticular process; stf, supratemporal fenestra.

are formed by the frontals. They project laterodorsad and are relatively short and very thick, with the dorsoposterior surfaces rather flat (Figs. 3, 4, 5B). They show a system of shallow grooves, lateromedially directed, that make the surface very different from the rugose nature of the muzzle. The structure of the horns is not very different in appearance from the horn cores present in bovids, although they are certainly not identical to the latter. The horns may have had a corneous covering, which would have made the horns much longer in life.

The *parietals* are fused to the frontals. Anteriorly, they are wide, forming a flat dorsal region. Centrally, the sagittal crest is thin and projects abruptly dorsad to form a posterodorsal process. This is axially thick and transversely wide, with a posterior projection extending over the conspicuous medial crest of the supraoccipital. From here, the supraoccipital crest extends ventrad to the squamosals. As a result, the supratemporal fenestra have low, lateral borders, whereas medially they have elevated borders. The anterolateral side of the parietals diverge outward, forming a strong basal structure for the horns and at the same time forming the posterior orbital wall.

The *supraoccipital* has a prominent posterior projection.

The *occipital crest* is transversely broad, although not as broad as the paraoccipital processes. The squamosals and parietals contribute to the high occipital crest, which in posterior view makes a continuous subcircular dome.

The *paraoccipital processes* are rather thin, directed partially towards the rear and a little downward, with the lateral projections modestly expanded.

The *occipital condyle* is robust, subspheric, with a marked ventral neck, and with the exoccipitals dorsolaterally directed, although no sutures are seen.

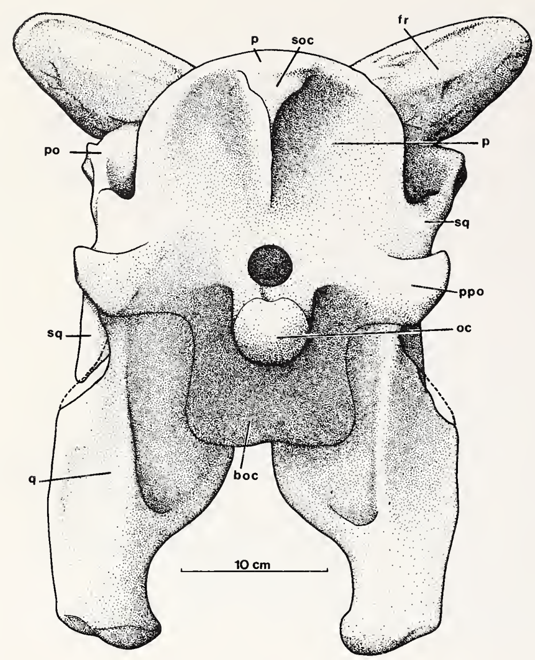

**Figure 4.** *Carnotaurus sastrei.* Skull in posterior view. Abbreviations as in Figures 2 and 3, and: boc, basioccipital.

## Lower Jaws

Both lower jaws (Figs. 2, 3) are completely preserved with all their teeth. Unfortunately some teeth were fragmented when the jaws were being separated from the skull.

The lower jaw is low and elongated (Figs. 2, 3), with the articular region and retroarticular process low and elongated in lateral view. It has a large mandibular fenestra and, behind it, on the internal side, a wide abductory fossa.

Externally, the postdentary bones have a smooth surface, whereas the dentary shows rugosities in the lower half, below the row of nutrient foramina. Above the foramina the bone surface is rather smooth.

The connection between the dentary–splenial and the postdentary bones is extremely weak. It is reduced to only two contact points, a dorsal one between the dentary and surangular, and a ventral one between a rod-like projection of the dentary and the angular (Fig. 2).

The *dentary* bears 13 teeth and 2 empty alveoli. The area of the jaw occupied by teeth is rather long. The posterior area of the dentary is bifurcate bordering a large mandibular fenestra. The posterodorsal projection of the dentary has a notch for an anterodorsal projection of the surangular.

The *splenial* is very near its original position against the right dentary (Fig. 3) and a bit moved relative to the left dentary. It is elongated and low, with the lower border progressively thicker towards the rear, where it forms most of the lower border of the jaw. The dorsal border is thin and fits into a special depression of the dentary. The anterior extension of this bone, which is dorsoventrally short, has an indentation that is related to the Meckelian cartilage. The posterior margin of the splenial is concave. The Meckelian foramen is present near the ventral border of this bone.

The *angular* is relatively small, forming the ventral border of the mandibular fenestra.

The *surangular* borders the mandibular fenestra dorsally and posteriorly. Its dorsal border is convex in lateral view. Posteriorly, near the angular, it has a 6-mm foramen, the "posterior surangular foramen" indicated for *Allosaurus* (Madsen, 1976: pl. 8). The posterior area of the surangular is low and elongated.

The *prearticular* is large, with the characteristic open "U" shape (Fig. 3B) defining an opening between its anterodorsal projection and the splenial. Its posterior projection, which is rather low, reaches the end of the retroarticular process.

The *articular* bears a well-developed medial projection. The glenoid has two concave facets for the quadrate condyles, with the axis directed anteromediad. The internal portion of the glenoid is larger and more defined than the external portion, and a clear longitudinal crest separates them. Posterior to the glenoid facet the dorsal portion of the retroarticular process is transversely concave. There is a postglenoid fossa between the glenoid and the dorsal area of the retroarticular process (Fig. 3B).

The *coronoid* is a small, elongate bone placed against the medial side of the surangular above the prearticular. Its dorsal border is transversely wide, and it has a lateral depression where the posterodorsal projection of the dentary inserts (Figs. 2, 3B).

## Hyoid Apparatus

Three pieces of the hyoid arch (Fig. 6) were found articulated between and within the lower jaws.

Anteriorly there is a corpus (see Romer and Parsons, 1978), which is flat, trapezoidal, and dorsally concave. On its posterior area there are two articular facets for the ceratobranchials (Ostrom, 1961). These are elongate, dorsally concave, and laterally convex.

## Comparisons of Skull and Lower Jaws

**Comparison with Tyrannosauridae.** The general plan of the skull and lower jaws of *Carnotaurus* is very different from that of the Laurasian Cretaceous carnosaurs. The genera *Tarbosaurus* (Maleev, 1955), *Daspletosaurus* and *Albertosaurus* (Russell, 1970), and *Tyrannosaurus* (Osborn, 1912) have the skull proportionally long and low, with the infratemporal fenestrae reduced by an anterior projection of the squamosal and quadratojugal. The region of the preorbital vacuity in these genera is anteroposteriorly large (Fig. 7K). In comparison, the skull of *Carnotaurus* is proportionally short and

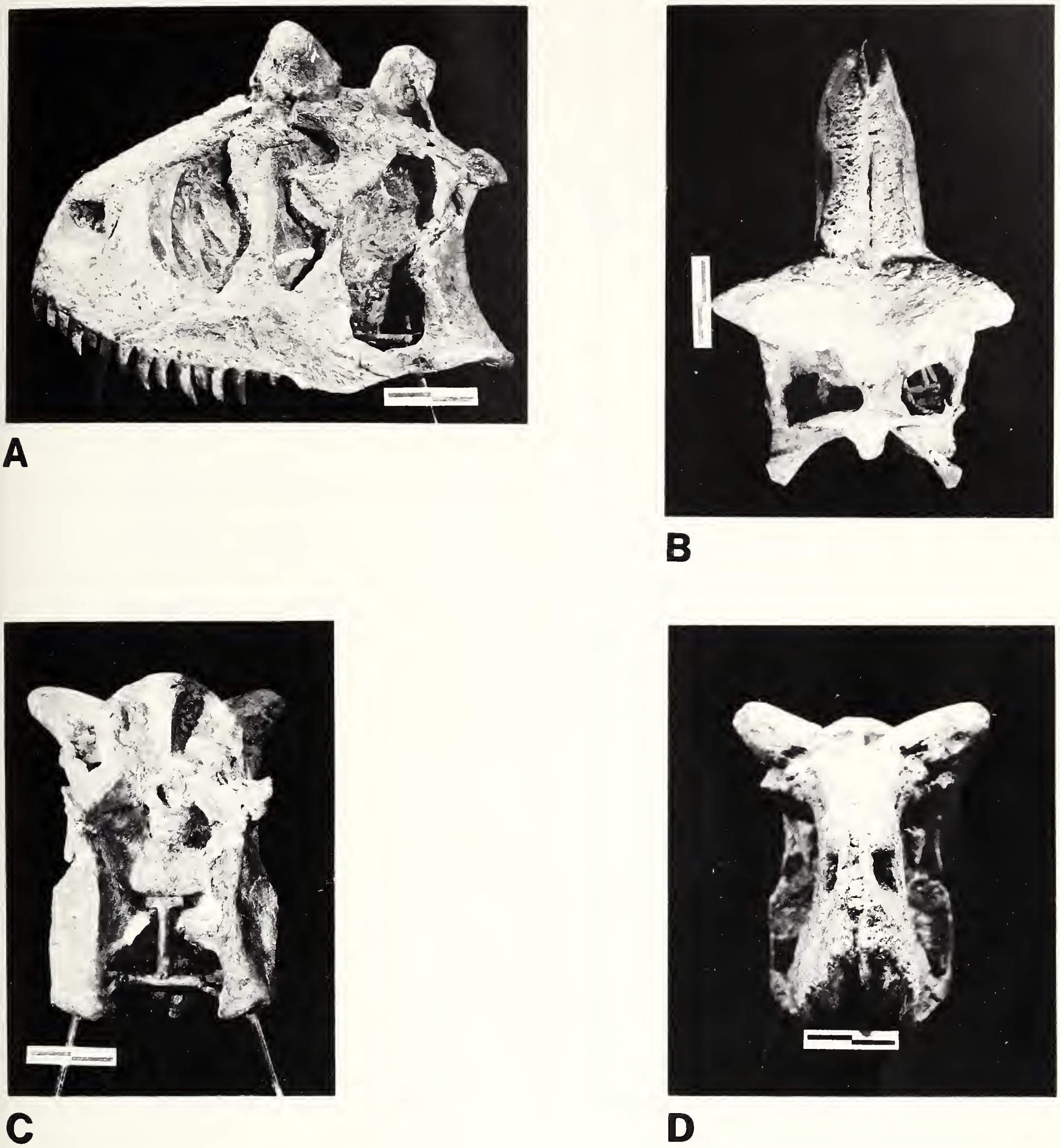

**Figure 5.** *Carnotaurus sastrei.* Skull in lateral (**A**), dorsal (**B**), posterior (**C**), and anterior (**D**) views. Scale = 10 cm.

very high, with a wide infratemporal fenestra. The preorbital vacuity is reduced anteroposteriorly, and the skull has well-developed frontal horns.

The lower jaws of *Carnotaurus* have large mandibular fenestrae, the retroarticulars are long and low, and the contacts between the dentary and the postdentary bones are limited.

These major differences between the *Carnotaurus* skull and jaws and those of the Tyrannosauridae suggest that two basically different adaptative models existed within the role of great predators. In detail, the main differences with the Tyrannosauridae are as follows:

a) Tyrannosaurids lack frontal horns.

b) The lachrymal of *Carnotaurus* does not have the pronounced anterior projection wedged between the maxilla and the nasal found in most of the Tyrannosauridae.

c) The lachrymal of *Carnotaurus* is posteriorly convex, not anteriorly convex as in the Tyrannosauridae.

d) The postorbital of *Carnotaurus* has a very short posterior projection, whereas in the Tyrannosauridae it is long.

e) The postorbital of *Carnotaurus* has a conspicuous anteroventral process that is very near the

Table 1. **Measurements (in millimeters) of the skull of *Carnotaurus sastrei*.**

| | |
|---|---|
| Skull | |
| Length of the skull from extremity of premaxilla to distal end of quadrate | 596 |
| Height of the skull from dorsal border of occipital crest to ventral border of jugal | 425 |
| Height of the skull from tip of the horn to ventral border of jugal | 434 |
| Distance from distal end of quadrate to top of parietal crest | 416 |
| Distance between tip of the frontal horns | 346 |
| Greatest expanse of paraoccipital processes | 245 |
| Greatest expanse of parietal crest | 185 |
| Transverse diameter of occipital condyle | 50 |
| Preorbital opening height | 172 |
| Preorbital opening length | 98 |
| Orbit height | 50 |
| Orbit length | 80 |
| Greatest length of quadrate | 221 |
| Jaw | |
| Total length of the jaw | 595 |
| Dentary length | 337 |
| Height of the jaw from dorsal border of surangular to ventral border of angular | 125 |

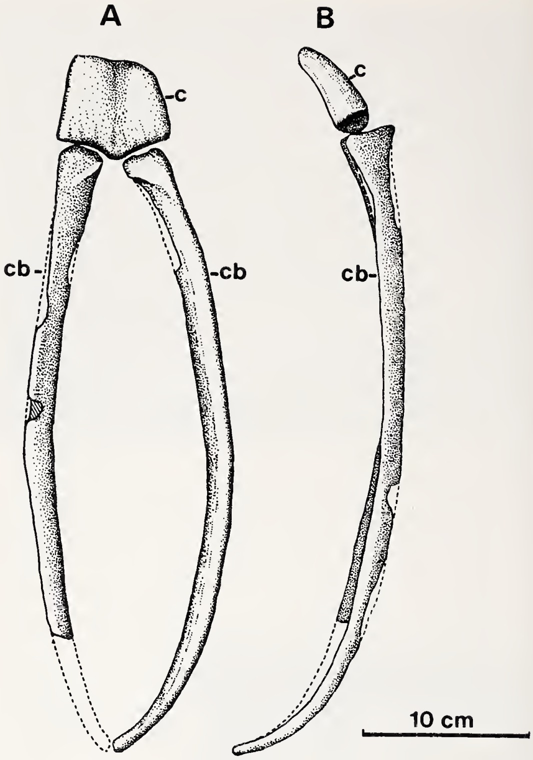

**Figure 6.** *Carnotaurus sastrei.* Hyoid arch in dorsal (**A**) and lateral (**B**) views. c, corpus; cb, ceratobranchial.

lachrymal, defining the ocular cavity and forming a well-defined opening.

f) The jugal of *Carnotaurus* does not have the typical anterior projection present in the Tyrannosauridae.

g) The squamosal and quadratojugal of *Carnotaurus* do not have the pronounced anterior projection (always present in the Tyrannosauridae) that virtually divides the infratemporal fenestra into two parts. In contrast, the squamosal of *Carnotaurus* has a rod-like ventral process that touches the anterior edge of the quadrate.

h) In *Carnotaurus* the quadrate is fused to the quadratojugal, and there is no indication of the quadrate foramen.

i) The development of the frontal horns resulted in strong modifications of the frontals, representing derived characters not developed within the Tyrannosauridae.

j) The pronounced axial crest of the supraoccipital, which dorsally contacts the dorsoposterior process of the parietals in *Carnotaurus,* is not present in the Tyrannosauridae.

k) The paraoccipital processes of *Carnotaurus* are long and slender, whereas in the Tyrannosauridae they are massive and robust (Fig. 7M).

l) The lower jaw of *Carnotaurus* has a large mandibular fenestra and only a weak contact between the dentary and postdentary bones. These are very different than those present in the Tyrannosauridae.

m) The posterior region of the *Carnotaurus* lower jaw is low and elongated, with the retroarticular process well defined and slender. These characters are very different from those of the Tyrannosauridae, where the lower jaw is high and the retroarticular process short and heavy.

**Comparison with Deinonychosauria.** The anatomical differences between *Carnotaurus* and Deinonychosauria skulls are significant and readily apparent; however, we will discuss some of them in detail as *Carnotaurus* and deinonychosaurs were contemporaneous theropods.

The infraorder Deinonychosauria is composed of the families Dromaeosauridae (Colbert and Russell, 1969), with the genera *Dromaeosaurus, Deinonychus* (Ostrum, 1969), and *Velociraptor;* and Troodontidae (Currie, 1987), with the genera *Saurornithoides* and *Troodon.* Both families, in spite of good anatomical differences that support their systematic validity (Osmolska, 1982), show a number of common characters.

A comparison of *Carnotaurus* with the Dromaeosauridae and Troodontidae shows outstanding differences in the skull and jaw. The more striking differences are as follows:

a) The deinonychosaurian skull is low and elongate, very different from that of *Carnotaurus.*

b) The parietal crest of deinonychosaurs is rather generalized, with plesiomorphic characters in its

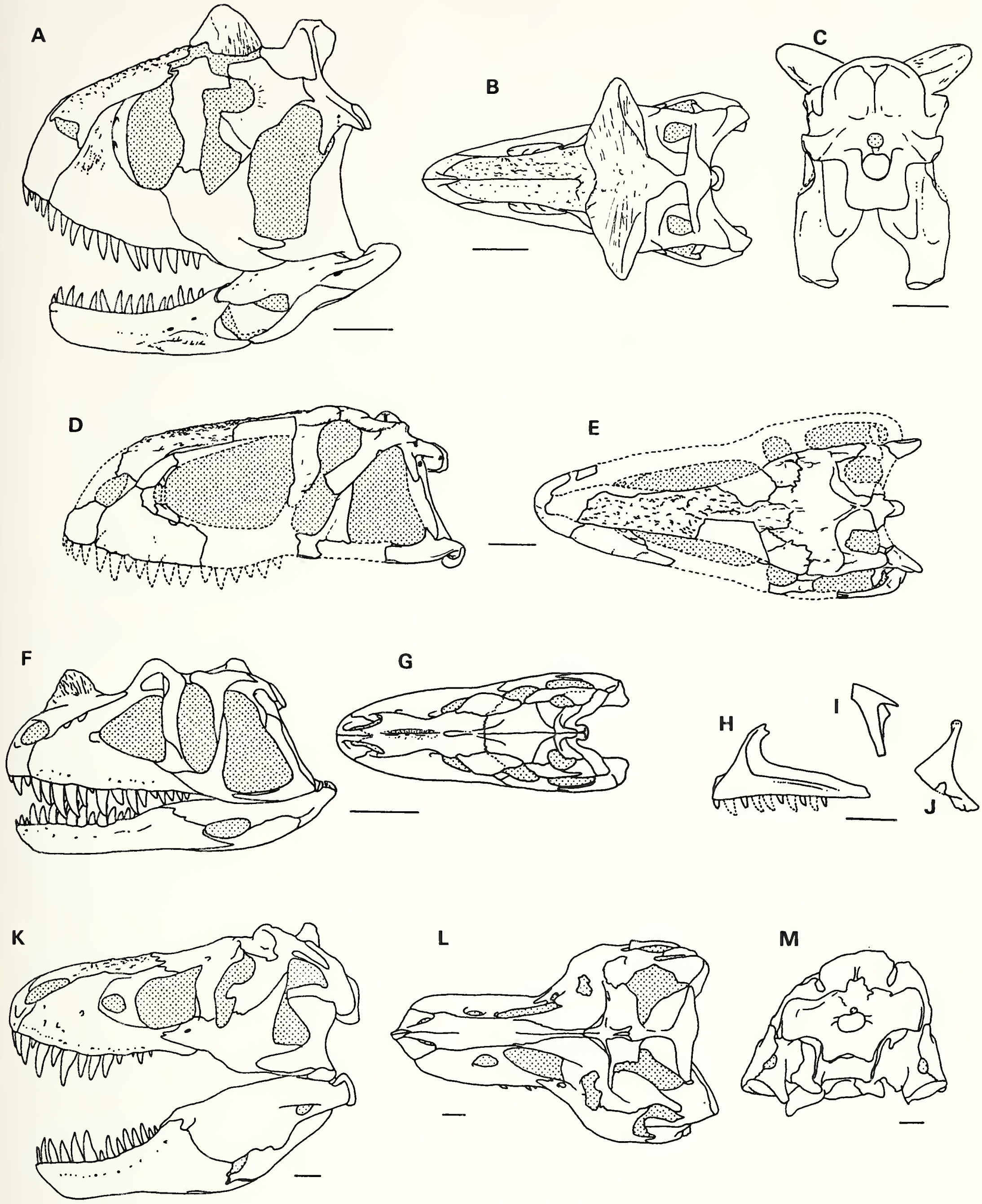

**Figure 7.** Skull and lower jaw of *Carnotaurus sastrei* (**A–C**) compared with *Abelisaurus comahuensis* (**D, E**), *Ceratosaurus nasicornis* (**F, G**), *Noasaurus leali* (**H–J**), and *Tyrannosaurus rex* (**K–M**), in lateral (**A, D, F, H–K**), dorsal (**B, E, G, L**), and posterior (**C, M**) views. H–J represent maxilla, squamosal, and quadrate of *Noasaurus leali* in lateral view. Scale = 10 cm, except for *Noasaurus leali* where scale = 2.5 cm.

thickness in linear projection. In *Carnotaurus* the parietal crest shows derived characters in the dorsal projection of its posterior area, reduction of its axial length, and anterolateral expansion as a result of the frontal horns.

c) The frontals of deinonychosaurs do not have any indication of osseous crests or horns.

d) In deinonychosaurs, the posterodorsal process of the premaxilla contacts the nasal, the anterior projection of the jugal borders the preorbital depression, and the anterior projection of the lachrymal has a long contact with the nasal and maxilla. None of these characters are present in *Carnotaurus.*

e) The condition of the quadrate and quadratojugal is plesiomorphic in deinonychosaurs as they are not fused and retain the quadrate foramen. In *Carnotaurus* such bones have the apomorphic condition of being fused, and the quadrate foramen is concealed.

There are more differences between deinonychosaurs and *Carnotaurus.* We consider those listed above sufficient to demonstrate that the skull of *Carnotaurus* is structurally and morphologically very different from that of the Deinonychosauria.

**Comparison with Ceratosauridae.** The comparison with *Ceratosaurus* (Gilmore, 1920), from the Upper Jurassic of North America, the only known genus of the family Ceratosauridae, results in an interesting picture of similarities. However, at least in reference to the skull, we do not interpret such similarities as indicators of an ancestor–descendant relationship, but rather as suggesting some degree of phylogenetic relationship. The more significant similarities are as follows:

a) The *Carnotaurus* premaxilla has a deep subnarial body, and the posterodorsal projection is reduced or absent, as in *Ceratosaurus.*

b) The additional preorbital opening in *Ceratosaurus* (according to Gilmore, 1920: pl. 18) is small and lies quite near the preorbital opening, as in *Carnotaurus.*

c) The infratemporal fenestra and the quadrate of *Ceratosaurus* and *Carnotaurus* are dorsoventrally large and do not show the typical anterior projections of the quadratojugal and squamosal of other theropods.

d) In Gilmore (1920: fig. 53), a dorsal projection of the parietals is seen that resembles the more derived condition of *Carnotaurus.*

These similarities are accompanied by significant differences, such as the proportions in the length and height of the skull of each genus, the absence in *Carnotaurus* of any nasal crest, and the absence in *Ceratosaurus* of any indication of a frontal or prefrontal osseous prominence. Also, in *Ceratosaurus,* the quadratojugal is not fused to the quadrate, and there is a well-developed quadrate foramen, whereas the opposite is true for *Carnotaurus.* The contact between the mandibular bones of the dentary and postdentary areas is rather firm in *Ceratosaurus,* but it is extremely weak in *Carnotaurus,* in which the mandibular fenestra is larger than the former.

**Comparison with Allosauridae.** There are a few similarities with *Allosaurus* (Madsen, 1976), the best known genus of the family Allosauridae. The most significant of these are as follows:

a) The deep premaxilla below the external nares.

b) The dorsal development of the posterior region of the parietals.

The differences are better expressed than the similarities. One very significant difference is that the squamosal, paraoccipital process, quadrate, and quadratojugal all show several derived characters not present in *Carnotaurus.* The squamosal of *Allosaurus* projects downward, the lateral end of the paraoccipital process is lower, and the quadrate is relatively shorter. Such morphological differences suggest that they represent very different adaptative types, although they may share a common ancestor older than Late Jurassic.

In the lower jaw, the differences between *Carnotaurus* and *Allosaurus* are very prominent because the mandibular fenestra is almost absent in the latter genus (Madsen, 1976: pl. 1).

**Comparison with Abelisauridae.** *Abelisaurus comahuensis* Bonaparte and Novas, 1985 (Fig. 7D, E), the type genus of the family Abelisauridae, from the Allen Formation, Lower Maastrichtian of Río Negro Province, Argentina, is a rather large theropod, with a skull of some 85 cm in total length. Although the skull of *Carnotaurus* has different proportions than the skull of *Abelisaurus* (short and high in the former, low and elongated in the latter), there are several common features that support allocation to the same family. They are the following:

a) The squamosal is very similar, especially in the shape and orientation of the ventral process, but with some differences in the posterior process.

b) The quadrate in both genera is long and fused to the quadratojugal.

c) The postorbital almost meets the lachrymal underneath the ocular cavity, although there are morphological differences in the anterior process of this bone between the genera.

d) The lachrymal is dorsoventrally convex towards the rear in each genus, and it contacts the postorbital above the orbit.

e) The shape and location of the additional preorbital opening is the same in both genera.

f) The premaxilla is deep below the narial opening in both genera.

g) The nasals show rugosities along most of the dorsal and lateral sides in both genera.

h) The posterior region of the parietal crest is elevated, and the supraoccipital bears a large dorsoventral keel in the axial plane, in both genera.

i) In dorsal view, the shape of the parietal crest is narrow posteriorly, widening anteriorly in both genera.

Of the common characters listed above, we consider that b, c, d, e, g, and i are synapomorphies of the family Abelisauridae. *Abelisaurus* and *Carnotaurus* are thus placed together in this family.

## AXIAL SKELETON

### Vertebral Column

The vertebral column of specimen MACN-CH 894 is complete and articulated from the atlas through the 6th caudal. The posterior caudals were de-

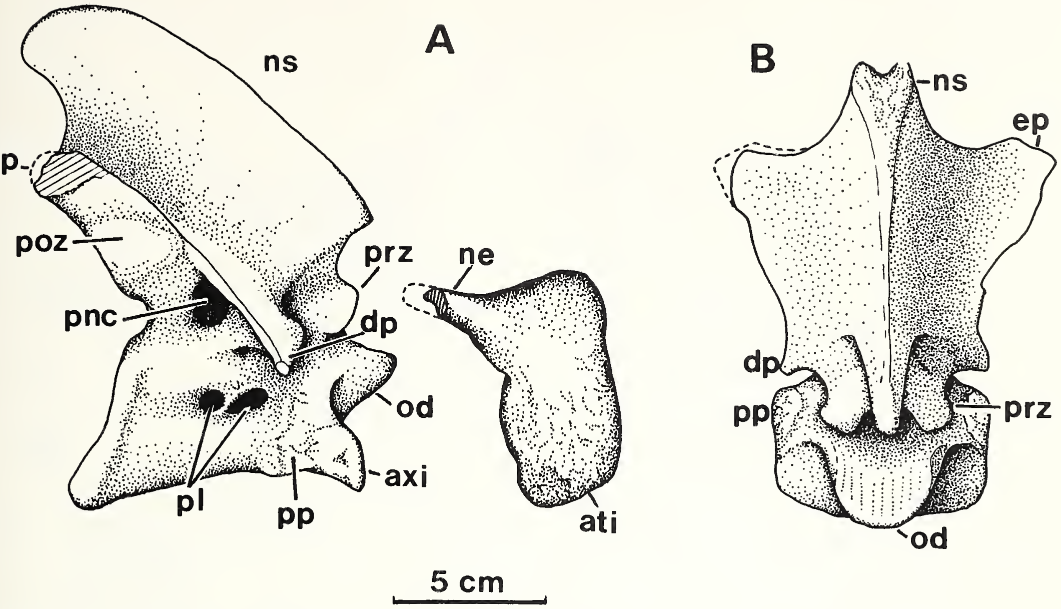

**Figure 8.** *Carnotaurus sastrei.* Atlas and axis in lateral view (A) and axis in dorsal view (B). ati, atlantal intercentrum; axi, axial intercentrum; dp, diapophysis; ep, epipophysis; ne, neurapophysis; ns, neural spine; od, odontoid process; pl, pleurocoel; pnc, pneumatic cavity; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis. Hatched area represents break; dashed lines represent estimated reconstruction.

stroyed by weathering, except the 12th, which is incomplete.

In general terms, the sequence of vertebrae is characterized by opisthocoelous cervicals with very reduced neural spines and very large epipophyses, and most of the dorsals are subamphiplatyan. The sacrum has seven fused vertebrae, and the anterior caudals have transverse processes projecting dorsolaterally.

**Cervical Vertebrae.** The *atlas* (Fig. 8A) has the intercentrum almost complete, and it is fused to the atlantal arches. The articular facet for the occipital condyle spreads onto most of the dorsal articular area and projects upward and forward. It does not show the articular facet for the odontoid as is seen in *Deinonychus* (Ostrom, 1969: fig. 26) but resembles the characters of *Ceratosaurus* (Gilmore, 1920: pl. 19) and *Allosaurus* (Madsen, 1976: pl. 11). In the ventral side of the intercentrum there are two processes (one on each side) for muscular attachments. On the posterior face the articular area for the axis intercentrum, which has a good suture with the centrum of the axis, is transversely wide, resembling the condition in *Ceratosaurus* and to a lesser extent that in *Allosaurus.* The atlantal arch is fused to the intercentrum and shows no indication of articulation with a proatlas, which may not have existed in *Carnotaurus.* The posterior projection is incomplete; the postzygapophysis is small. In posterior view the lower side of the roof made by the atlantal arches has a subcircular cavity for the passage of the spinal chord. Mobility between the atlas and axis appears to have been small in this genus.

The *axis* (Fig. 8A, B) is complete and shows little deformation. The centrum and intercentrum are relatively elongated, but with rather modest transverse and dorsoventral diameters.

In anterior view the continuous surface for articulation with the atlas and the odontoid articulation for the occipital condyle are seen. The posterior face of the centrum is very concave, with the lower area projected posteriorly. In ventral view the axis bears a poorly defined, rather vestigial keel. In lateral view two small pleurocoels are present in the upper half of the centrum. A well-defined cavity, subdivided into two, lies behind and a bit dorsal to the diapophyses, and two depressions with foramina are located above and behind the prezygapophysis. The depressions with foramina that penetrate the axis probably correspond to a system of pneumatic cavities as in *Piatnitzkysaurus floresi* (Bonaparte, 1986a).

The prezygapophysis is small, whereas the postzygapophysis is large with the longest axis transversely placed. The parapophysis is not defined, although it may correspond to the suture between the intercentrum and the centrum. The diapophysis is rather small.

The blade of the neural spine is large with the dorsal border convex in lateral view, as in *Ceratosaurus* (Gilmore, 1920: pl. 19). This border is slightly forked at the posterdorsal end in dorsal view. Below it a division follows to the epipophy-

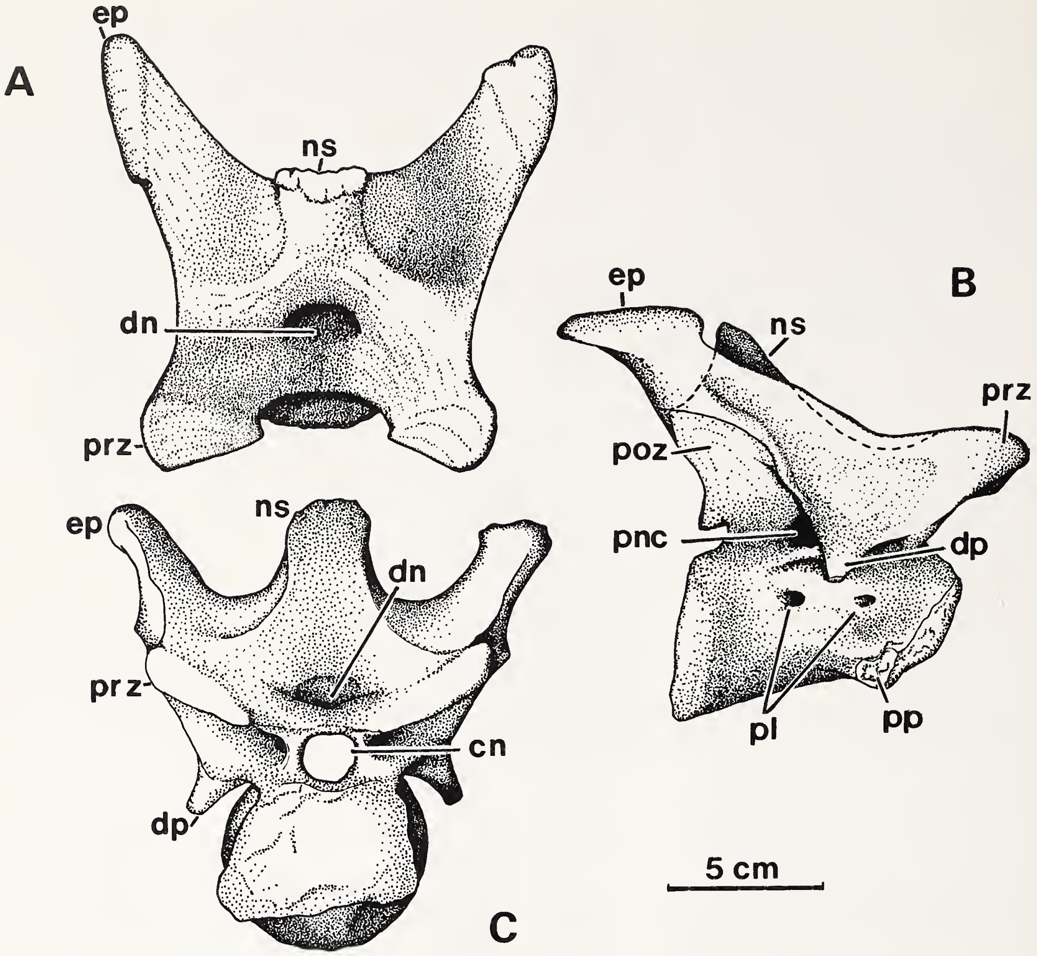

**Figure 9.** *Carnotaurus sastrei.* Third cervical vertebra in dorsal (**A**), lateral (**B**), and anterior (**C**) views. Outline of neural spine in lateral view indicated by dashed lines. Abbreviations as in Figure 8, and: cn, neural canal; dn, depression.

seal area. In posterior view there is a deep depression with foramina in the axial plane below the neural spine and a wide, deep depression with foramina above the neural canal. The axis is markedly different in almost all details from that of *Tyrannosaurus* (Osborn, 1917). It is, however, very similar to that of *Ceratosaurus* and, to a lesser degree, *Allosaurus* (Madsen, 1976: pl. 11).

The *third cervical* (Fig. 9) is complete and, like the remaining cervicals, is characterized by a significant reduction of the neural spine and hypertrophy of the epipophysis.

In lateral view the anterior face of the centrum makes a sharp angle with the anteroposterior plane, indicating the limits of the dorsoventral flexion of the neck.

There are two small pleurocoels on the rather flat lateral side of the centrum. The lower border of the centrum is almost straight. Behind and above the diapophysis there is a large depression and a foramen passing into the neural arch. Anterior to the diapophysis there is a modest foramen. Both the parapophysis and diapophysis are of modest size. The epipophysis is strongly developed, and a lamina connects it to the prezygapophysis. This lamina sharply delimits the lateral and dorsal areas of the neural arch. In lateral view, the neural spine is a bit lower than the epipophysis. The prezygapophyses are well separated from one another, each having the major axis transversely directed and each inclined towards the axial plane.

In posterior view a large cavity is exposed that leads into the neural arch. In the axial area there is a rugose zone for insertion of intervertebral ligaments. The posterior concavity of the centrum is deep, with its geometric center moved to the upper half. In dorsal view this vertebra is rather flat with wide laminar surfaces.

The *fourth cervical* is basically the same as the 3rd cervical, but larger. The ventral border of the centrum is more curved, the parapophysis better defined, and the diapophysis thicker. The cavities and foramina for the pneumatic system are similar, except that the one behind the diapophysis is larger.

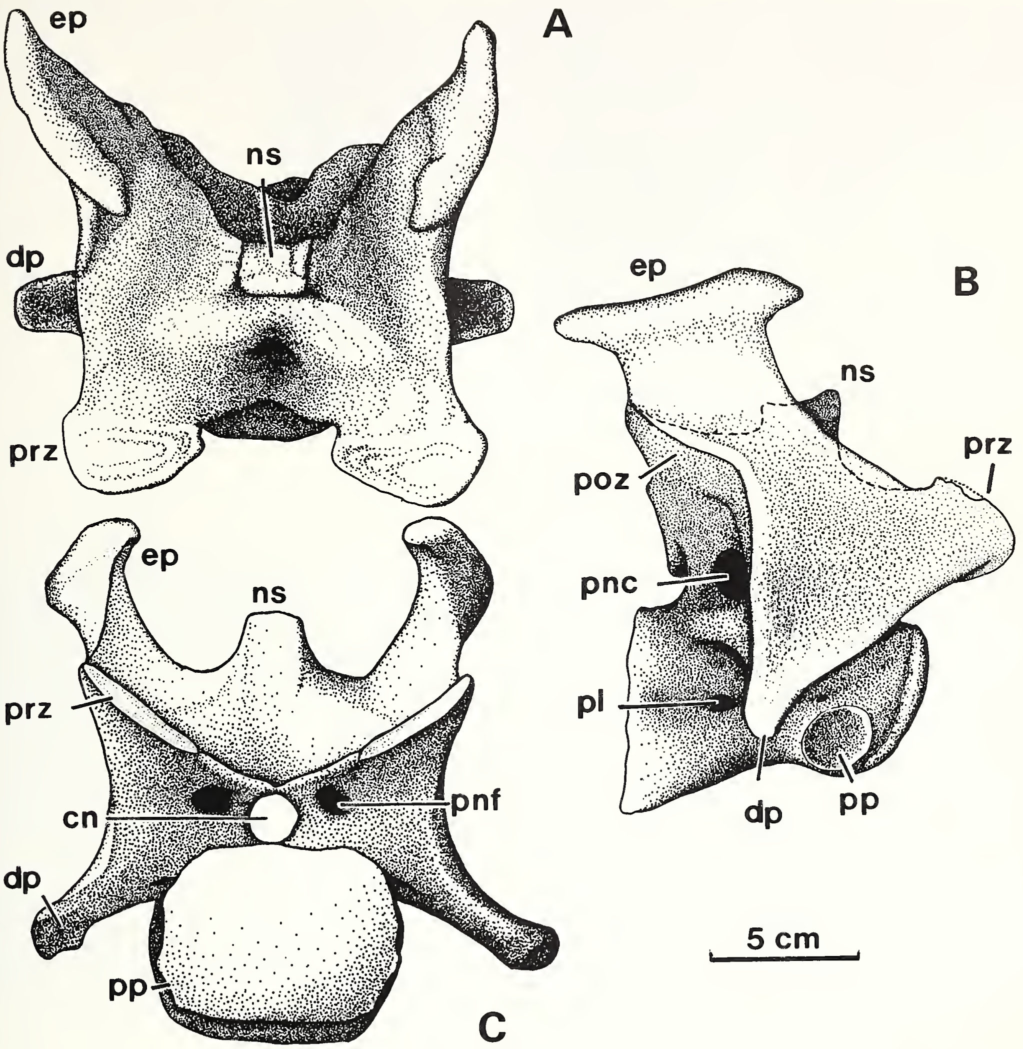

**Figure 10.** *Carnotaurus sastrei.* Sixth cervical vertebra in dorsal (**A**), lateral (**B**), and anterior (C) views. Abbreviations as in Figures 8 and 9, and: pnf, pneumatic foramen.

The postzygapophyses are larger and the epipophyses are axially longer, with a posteriorly well-defined process and an incipient anterior process. In anterior view the neural spine is more reduced than in the 3rd cervical. There is a depression on the dorsal surface in front of the reduced neural spine and another one between the neural spine and the dorsal projection of the epipophysis.

The *fifth cervical* is larger than the 4th cervical, especially in the volume of the centrum. The diapophysis is more robust, and the epipophysis has the anterior and posterior processes more defined. Also, the lamina that extends between the epipophysis and prezygapophysis is higher and more laterally placed. The system of depressions and foramina of the pneumatic cavities is similar to that of the 4th cervical.

The *sixth cervical* (Figs. 10, 11) is a little larger than the 5th cervical. In the centrum the inclinations of the anterior and posterior faces are more pronounced. The epipophyses are better developed anteroposteriorly, and the postzygapophyses are well separated.

The *seventh cervical* is essentially the same as the 6th cervical, although more robust. The postzygapophysis is larger, with the larger dimension transversely placed and the articular facet directed obliquely ventromediad. In posterior view the wide depression behind the neural spine has two rather large fenestrae that lead into the neural arch. Posteriorly, the centrum is subcircular and less concave than in the 6th cervical.

The *eighth cervical* vertebra is more voluminous and higher than the 7th cervical. The centrum is

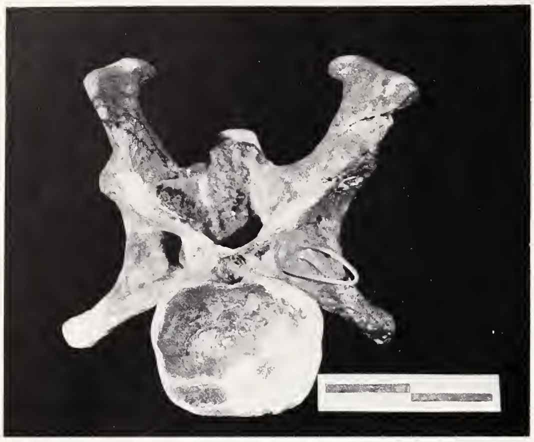

**Figure 11.** *Carnotaurus sastrei.* Sixth cervical vertebra in posterior view. Scale = 10 cm.

slightly concave on its ventral side, as in the preceding ones, and it lacks a keel. In the area of the pleurocoel there is a depression and three foramina penetrate the centrum. The neural spine is almost nonexistent, and the epipophysis is more elevated than in the 7th cervical. The diapophysis is a little higher, and the opisthocoelia is less pronounced.

The *ninth cervical* (Fig. 12) is larger than the 8th cervical, although it shows generally the same morphology. In comparison, however, the opisthocoelia is less pronounced, the diapophyses are more elevated and stronger, and the neural spine is a little more developed. The system of depressions, foramina, and pneumatic cavities appears to be the same, but with larger foramina. A ventral, rounded keel is present on the centrum, with slight depressions on each side of it.

The *tenth cervical* (Fig. 13) has a centrum with the anterior and posterior articulations at a right angle with respect to the horizontal axis. A modest keel exists on the ventral border. The diapophysis is more elevated, more robust, and longer than in the 9th cervical. The neural spine is also higher, although it remains lower than the epipophysis. The latter shows some reduction, with the anterior and posterior processes very reduced. On the posterior side of the neural spine there are strong rugosities for the attachment of interspinous ligaments.

**Dorsal Vertebrae.** The *first dorsal* vertebra was affected by a small fault in the rock that produced some displacement and deformation in its neural arch. The centrum is almost the same, except for a larger "pleurocoelus depression," and the parapophysis is more dorsally placed.

In the neural arch the changes in relation to the last cervical are abrupt. There is no epipophysis, the neural spine is the highest dorsal element of the vertebra, and the robust transverse process is at the level of the zygapophyses. However, the morphology and orientation of the zygapophyses are similar to those of the cervicals. The total height of the vertebra is greater than the 10th cervical. Comparatively, the shallow opisthocoelia of the last cervical and first dorsal are very different to the marked opisthocoelia of the same vertebrae of *Allosaurus* (Madsen, 1976: pl. 15).

The *second dorsal* (Fig. 14) has the transverse process more elevated and robust than in the 1st dorsal, and the neural spine is a little larger. The zygapophyses are nearer to the axial plane, in particular the postzygapophyses, which show an incipient hyposphene. In lateral view, two borders are present on the ventral side of the transverse process: the anterior and posterior infradiapophysial laminae. A noticeable depression penetrating into the neural arch is present between the anterior infradiapophysial lamina and the prezygapophysis.

The *third dorsal* is like the 2nd dorsal, but the neural spine is longer and more robust and the transverse process longer. The zygapophyses are less inclined, particularly the postzygapophysis, which is almost horizontal. Below the postzygapophysis is a well-developed hyposphene. Underneath the prezygapophysis there is a column-like process, which borders laterally a large depression that communicates with the neural arch.

The *fourth dorsal* (Fig. 15) has a longer neural spine than the 3rd dorsal, which is also anteroposteriorly flat and posteriorly inclined. The prezygapophysis is subhorizontal and projects anteriad. The postzygapophysis is horizontal, and the lateral border is directed downward. The hyposphene of this vertebra is well developed and forms a wide body that reaches the roof of the neural canal. The parapophysis is dorsal to the vertebral body.

In the *fifth dorsal* (Fig. 16) the parapophysis is in a very different position—approximately in the middle of the neural arch and projecting laterad. The parapophysis borders a large cavity that penetrates into the neural arch, in contrast with the condition in the 4th dorsal. The neural spine is large, in part laterally compressed, and with a dorsal expansion. The centrum is almost amphiplatyan.

In the *sixth dorsal,* and to a degree in the 5th dorsal, below the prezygapophysis there is a lower, anterior projection. The parapophysis is more dorsally placed, and it has a long, laterally projecting stem. Between the parapophysis stem and the diapophysis there is a very large fossa communicating into the neural arch. In dorsal view the transverse process has a wide, flat surface. The centrum of this vertebra has a lateral depression oriented anteroposteriorly just below the union of the centrum with the neural arch. Two conspicuous foramina are located there. Along most of its perimeter the posterior border of the centrum is pathologically hypertrophied.

The *seventh, eighth,* and *ninth dorsals* (Figs. 17, 18) are of similar morphology. The 7th dorsal is a bit taller than the 6th dorsal, and the process below the prezygapophysis persists. The postzygapophysis is transversely concave. In the neural spine, there are strong osseous processes for the attachment of

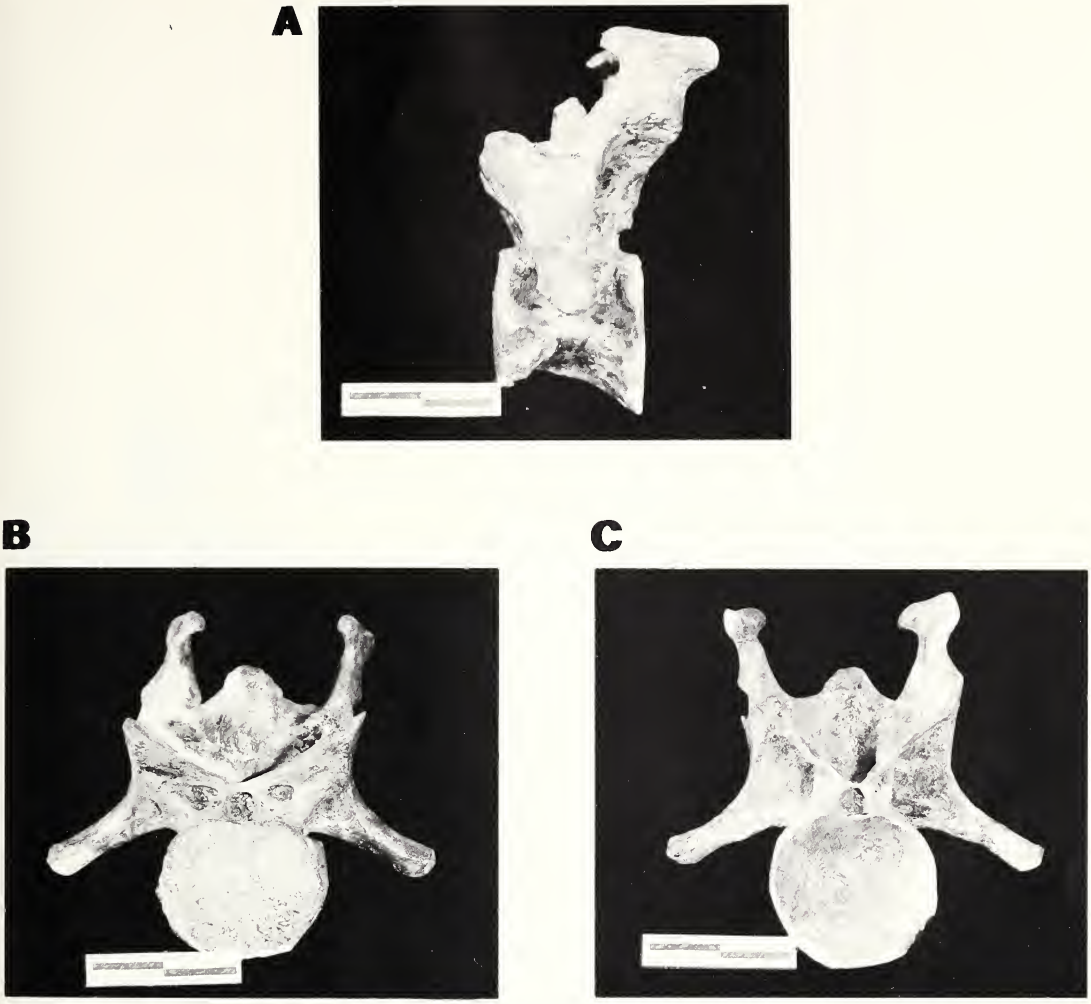

**Figure 12.** *Carnotaurus sastrei.* Ninth cervical vertebra in lateral (**A**), anterior (**B**), and posterior (**C**) views. Scale = 10 cm.

tendons. In the 8th dorsal, the dorsal surface of the transverse processes is larger than in the 7th dorsal, and it is even more so in the 9th.

The *tenth* and *eleventh dorsals* (Figs. 19, 20) have centra of greater diameter than the preceding vertebrae. The parapophysis, very dorsal in position, tends to become part of the dorsal lamina of the diapophysis. The parapophysis, is larger anteroposteriorly than in previous vertebrae, increasing its surface posteriorly. The neural spine of the 10th dorsal does not show the conspicuous osseous rugosities for attachment of tendons, but they are present in the 11th. The prezygapophysis of the 11th dorsal is reduced and suggests that the movements between the 10th and 11th vertebrae were very restricted.

**Sacral Vertebrae.** The sacrum of *Carnotaurus* is almost complete, except for the system of platelike sacral ribs that was not well preserved. The sacrum consists of seven vertebrae, of which the 1st sacral is fused only in the vicinity of the postzygapophysis and the following six are intimately fused (see Fig. 20). The 1st sacral preserves most of the characters of the last dorsals, but the transverse processes are reduced, both in length and width. The neural spine is axially reduced, and the lateral cavities of the neural arch are concealed.

The 2nd to 7th sacral vertebrae are strongly fused, both through the centra and through the neural arches. The neural spines, especially distally, form a continuous ossification. The co-ossified centra form, in lateral view, a dorsally convex arch. In ventral view, the centra in the middle of the sacrum (sacrals 3, 4, and 5) are transversely reduced, particularly the 4th sacral. There is thus a marked reduction of volume in the vertebral bodies of the sacrum.

The lateral projections of the sacrum are short,

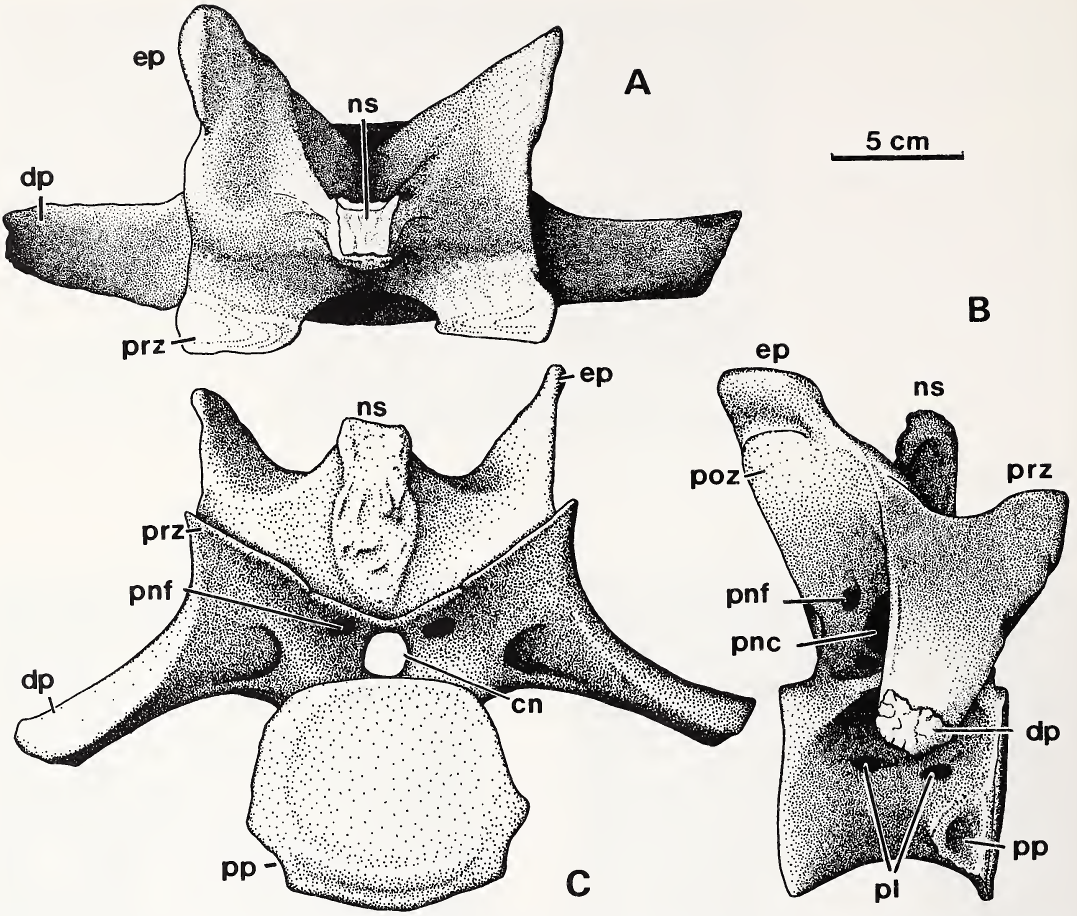

**Figure 13.** *Carnotaurus sastrei.* Tenth cervical vertebra in dorsal (**A**), lateral (**B**), and anterior (**C**) views. Abbreviations as in Figures 8 and 9.

indicating that the pelvis of *Carnotaurus* was narrow. The main connection between the sacrum and the ilia was through the transverse processes. The sacral ribs are incomplete, but appear to be very short. From the 3rd sacral distad they are rather thick in cross section.

**Caudal Vertebrae** (Figs. 21–23). Only six proximal, articulated caudals are preserved, with some of them showing effects of weathering. Also preserved is an isolated centrum with part of the neural arch, possibly the 12th caudal.

The first two caudals are very large and robust. The caudals rapidly decrease in size posteriorly to the 5th, and the centrum of each is amphicoelous. Elongation of the vertebral bodies is apparent, and the centra show only slight lateral depressions.

The dorsolaterally projecting transverse processes reach a level very near the top of the neural spine, suggesting a derived condition. The lower surface of the transverse process faces ventrolaterally. Another curious, derived character seen in the available caudals is the expanded distal end of the transverse process. This feature is present in the six proximal caudals, whereas in the 12th caudal it is not preserved.

**Comparison of Vertebral Column.** The presacral vertebrae of *Carnotaurus sastrei* correspond well with the general model present in the Theropoda, particularly in the Carnosauria. However, they bear several derived characters that readily distinguish them from the known theropods, except perhaps *Noaşaurus leali* (Bonaparte and Powell, 1980).

The cervicals of *Carnotaurus,* posterior to the axis and up to the 10th, show a strong reduction of the neural spine and a strong dorsal development of the epipophyses, which form a paired row of neural spine-like processes. This model of cervical vertebrae was undoubtedly adapted for quite a new arrangement of the muscular system, related to better functional control of neck and cranial movements. It resembles in part the neck morphology of the Ornithomimidae, in which the neural spine is vestigial and bears dorsolateral processes higher than the neural spine.

In *Allosaurus fragilis* the 4th and 7th cervicals show the lateral lamina connecting the epipophysis

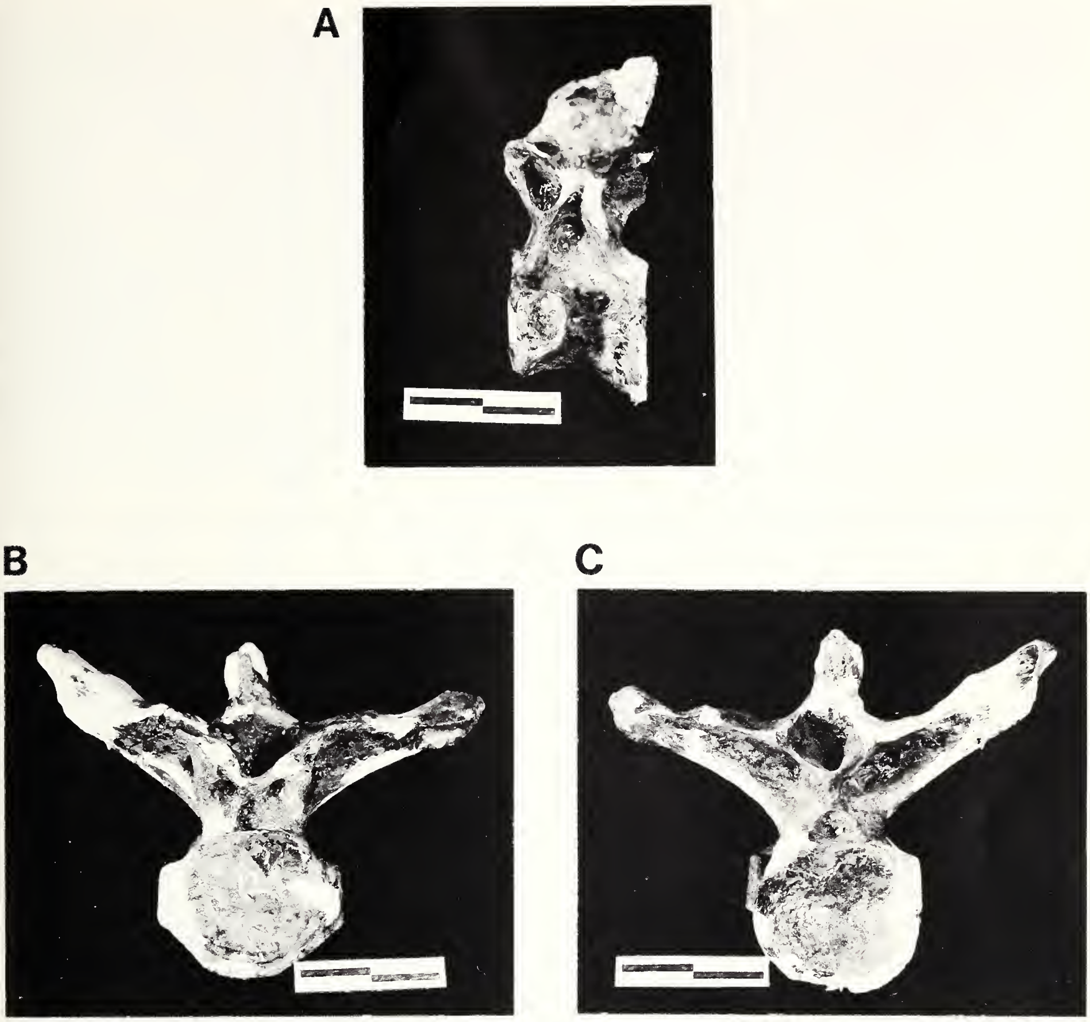

**Figure 14.** *Carnotaurus sastrei.* Second dorsal vertebra in lateral (A), anterior (B), and posterior (C) views. Scale = 10 cm.

with the prezygapophysis, and the 5th cervical shows good dorsal development of the epipophysis (Madsen, 1976: pl. 13), although it is less developed than in *Carnotaurus.* However, the anatomy of these vertebrae of *Allosaurus* suggests that, at least in part, the unique anatomy of the cervicals of *Carnotaurus* were roughly outlined in *Allosaurus.*

The dorsal vertebrae are significantly different in the lateral structure of the neural arch from those of the Tyrannosauridae, Allosauridae, Ceratosauridae, and *Deinonychus.* The differences relate to the higher position of the parapophyses in *Carnotaurus,* which increases from the 5th dorsal posteriorly to reach their highest point in the 10th and 11th dorsals, in which diapophyses and parapophyses are very near one another in the horizontal plane. Thus, the dorsal migration of the parapophyses of *Carnotaurus* led to several autopomorphies of the Patagonian form, *i.e.,* anteroposteriorly wide transverse processes, presence of a discrete fossa between the parapophyses and the infradiapophysial lamina, and presence of a well-defined lamina between the parapophysis and dorsolateral border of the centrum.

In contrast to the similarities of the skull and axis discussed previously, no shared derived characters have been seen in the presacral vertebrae of *Carnotaurus* and *Ceratosaurus.*

The count of seven sacral vertebrae and the presence of a six-vertebrae synsacrum represent significant derived characters not recorded, as far as we know, in other Carnosauria. However, a comparable number of sacrals is present in some small theropods, such as *Saurornithoides* (Barsbold, 1974). Osborn (1917) recognized five sacral vertebrae in *Tyrannosaurus,* although from the figure

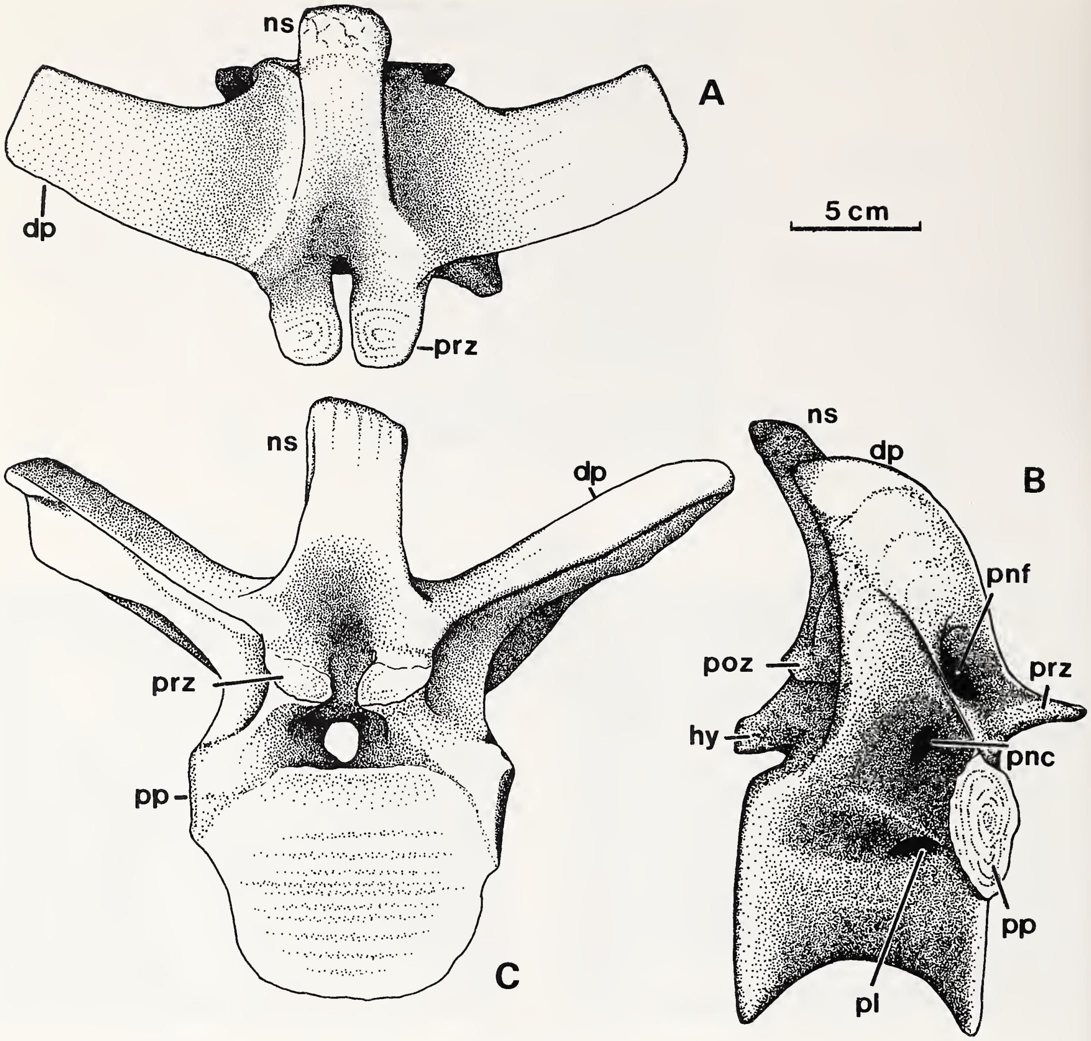

**Figure 15.** *Carnotaurus sastrei.* Fourth dorsal vertebra in dorsal (**A**), lateral (**B**), and anterior (**C**) views. Abbreviations as in Figures 8 and 9, and: hy, hyposphene.

of the pelvis and sacrum in lateral view we suspect that the 13th dorsal may very well be the first functional sacral because of its position "within" the ilia, even though it is not fused to the remaining sacrals. In Osborn's paper (1917: fig. 19) one can see that the sacrum of *Tyrannosaurus* is proportionally shorter than that of *Carnotaurus*, and it is wider at both ends. Also, it is possible to see that it has neither the dorsal arching along the ventral border of the centra nor along the row of sacral ribs. Even though the co-ossified dorsal end of the neural spines is a common character for *Tyrannosaurus* and *Carnotaurus*, the arching of the centra and the line of union between the sacrum and ilia (see Fig. 20), as well as the strong co-ossification of the centra and their reduced thickness, represent a set of derived characters not present in *Tyrannosaurus*. This suggests that the sacrum of the Patagonian genus is more derived than that of the tyrannosaurids.

*Piatnitskysaurus* and *Allosaurus* clearly have more primitive sacra (Gilmore, 1920; Madsen, 1976; Bonaparte, 1986a), each with five vertebrae that are not completely fused.

*Ceratosaurus* shows similarities in the general plan and in several derived characters. The sacrum is composed of five fused vertebrae (Gilmore, 1920), which are well co-ossified, as in *Carnotaurus*. In addition, in *Ceratosaurus* reduction of the thickness of the fused centra is also similar to the situation in *Carnotaurus*. Gilmore considered the sacral vertebrae of *Ceratosaurus* to number five, taking into account only the fused ones. In our opinion the functional sacral vertebrae of this North Amer-

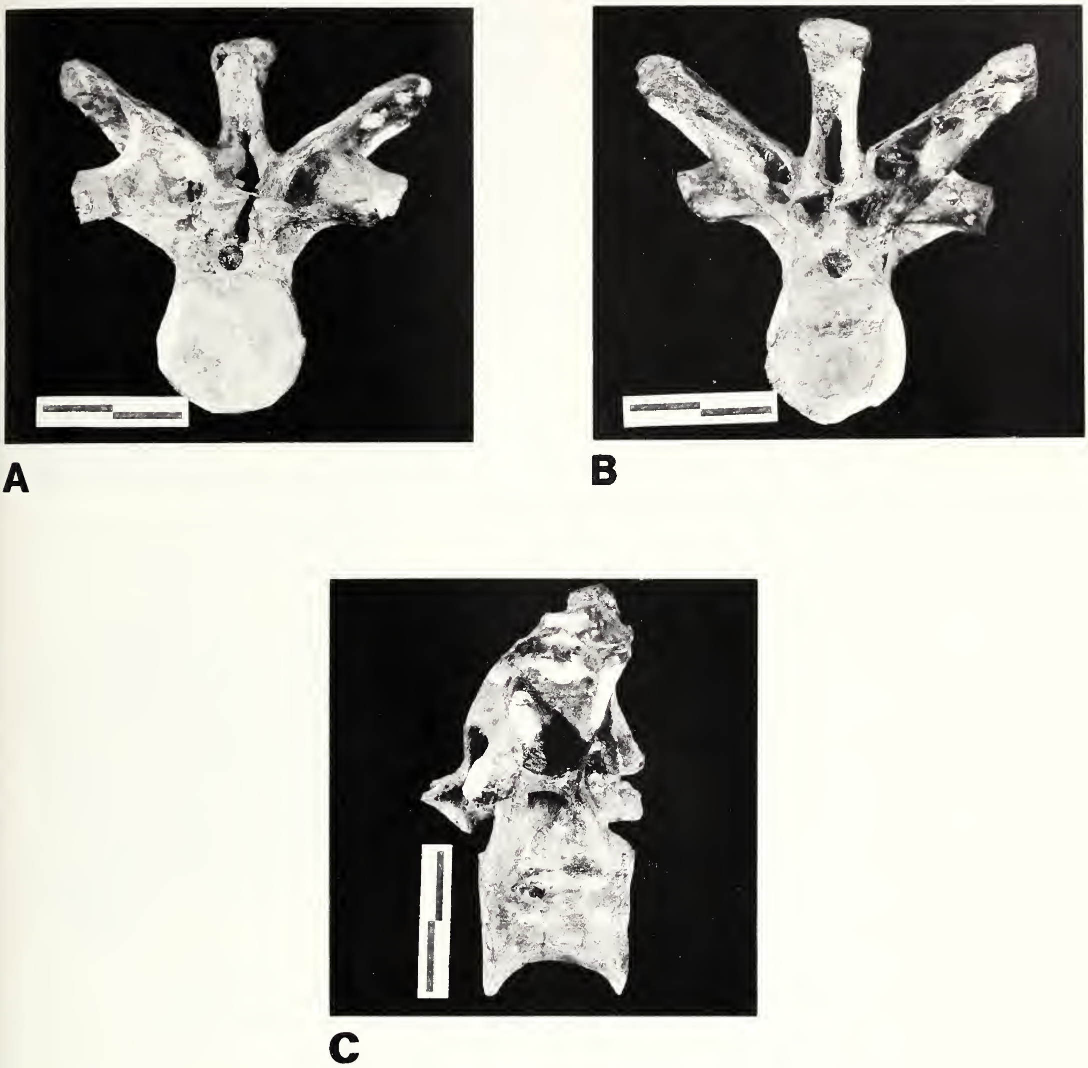

**Figure 16.** *Carnotaurus sastrei.* Fifth dorsal vertebra in anterior (**A**), posterior (**B**), and lateral (**C**) views. Scale = 10 cm.

ican Morrison Formation genus includes seven and possibly eight vertebrae, including the last two presacrals and possibly the first caudal of Gilmore. The seven sacral vertebrae of *Carnotaurus,* with the 1st sacral "recently" incorporated from the dorsals (note the intermediate morphology of this vertebra and its partial fusion with the posterior sacrals [see Fig. 20]), suggest that general organization of the sacrum is rather similar to that of *Ceratosaurus.* The similarities in the sacrum of these two genera strongly suggest a common trend of specialization that may reflect a close phylogenetic relationship.

Concerning the caudal vertebrae, we are not aware of comparable characters in other theropods. It suggests that both uncinate processes and laterally elevated transverse processes may represent an autapomorphy of *Carnotaurus.*

## Ribs

The complete series of cervical ribs and most of the dorsal ribs are preserved. The *atlantal rib* (Fig. 24A) has an articular head with a slightly flat expansion, but without indication of a separate capitulum or tuberculum. The stem is long, rather flat, and reaches the 4th cervical vertebra.

The *second rib* is larger and has a more defined proximal area. The shaft is rather flat until the 3rd vertebra, behind which it extends stiliform to the 5th cervical vertebra.

The *third cervical rib* (Fig. 24B) shows a well-defined capitulum and tuberculum. The latter forms an expanded dorsal process. A short anterior process that increases in size in the following ribs is present. The shaft of this rib is very long, almost

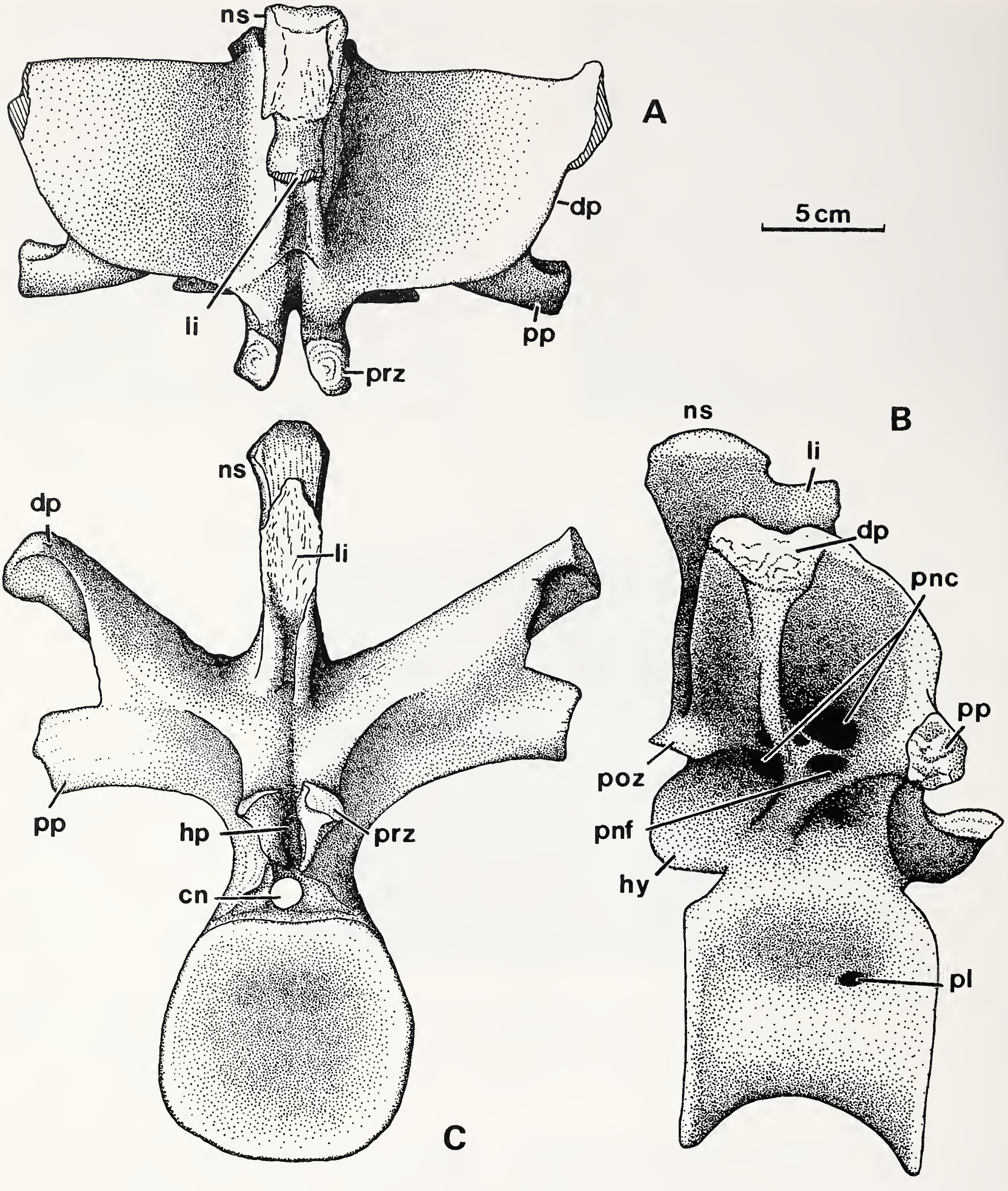

**Figure 17.** *Carnotaurus sastrei.* Eighth dorsal vertebra in dorsal (**A**), lateral (**B**), and anterior (**C**) views. Abbreviations as in Figures 8, 9, and 15, and: hp, hypanthrum; li, scar for interspinous ligaments.

reaching the 7th cervical vertebra. The proximal area of the shaft is laterally convex and continues distad as a subcylindrical rod of constant diameter.

The *fourth cervical rib* (Fig. 24C) is similar to the previous one, but the proximal laminar area is larger, followed posteriorly by an elongate and delicate stilet.

The shape of the 4th cervical rib is repeated up to the 9th cervical rib (see Fig. 24D, E). The anterior process remains conspicuous, and each rib possesses a well-defined capitulum and tuberculum.

In the *tenth cervical rib* a lamina connects the capitulum and tuberculum. The anterior process is abruptly reduced, and there is no distinction in the shaft between the proximal and distal portions. The shaft of this rib is relatively short and thick.

The *first dorsal rib* (Fig. 25A, B) is much longer and thicker, and it has a large capitulum and robust

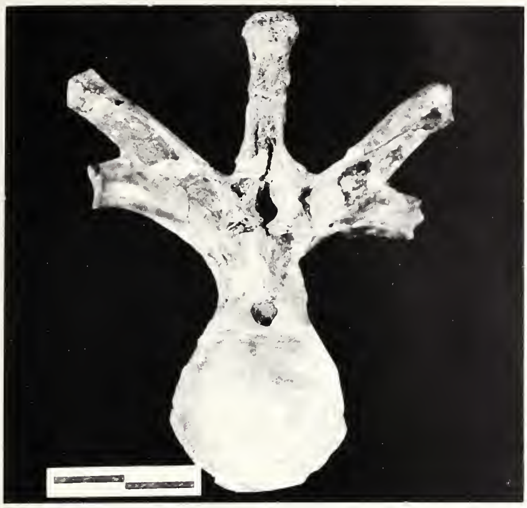

**Figure 18.** *Carnotaurus sastrei.* Eighth dorsal vertebra in posterior view. Scale = 10 cm.

tuberculum. The *second dorsal* is similar, but larger, with a larger and stronger proximal process. The *third* and *fourth dorsal ribs* (Fig. 25C, D and E, F, respectively) increase in size. The size of the proximal region of each rib decreases posteriorly, and the shaft of the capitulum becomes shorter because of the dorsal migration of the parapophysis. The *last dorsal,* the 11th (Fig. 25I, J), is short and in the living animal would have almost touched the anterior border of the ilia.

### Gastralia

Because of weathering and the nature of the excavation process, the gastralia, which were in their original position, were not properly recovered. They were positioned from very near the anterior border of the pubis forward and consisted of rather long, subcylindrical rods, lying transversely very near one another.

### Haemal Arches

The anterior haemal arches (Fig. 26) are represented by natural molds and bone fragments (one with the proximal part preserved and another one complete). They are proportionately long and slender, with a relatively wide proximal articulation and the haemal canal enclosed dorsally. The articular facets and the shape of the haemal canal suggest that the haemapophyses had a more posterior than ventral orientation.

In the anterior part, the haemal canal has a lateral expansion, whereas posteriorly the canal shows a deep distal depression. These features indicate that the haemal canal had an oblique position relative to the long axis of the shaft of the haemapophysis. These features suggest that natural position of the haemapophysis was far from perpendicular to the axis of the tail and that it more probably formed a very acute angle with it. It also means that the tail of *Carnotaurus* was probably dorsoventraly flattened.

**Table 2.** **Measurements (in millimeters) of presacral, sacral, and caudal vertebrae of *Carnotaurus sastrei.***

| Vertebra number | Maximum length of centra | Maximum width (anterior) of centra | Maximum height (anterior) of centra | Greatest height overall |
|---|---|---|---|---|
| Presacrals | | | | |
| Atlas | 45 | 83 | 40 | 95a |
| Axis | 118 | 84 | 55 | 198 |
| 3 | 100 | 68 | 41 | 175† |
| 4 | 110 | 71 | 50 | 187† |
| 5 | 119 | 82 | 56 | 210a† |
| 6 | 120 | 92 | 67 | 225† |
| 7 | 110 | 97 | 70 | 226† |
| 8 | 108 | 105 | 87 | 250† |
| 9 | 104 | 111 | 96 | 265† |
| 10 | 98 | 115 | 106 | 245† |
| 11 | 100 | 114 | — | 256 |
| 12 | 101 | 112 | 108 | 257 |
| 13 | 103 | 120 | — | — |
| 14 | 108 | 110 | 105a | 276 |
| 15 | 101 | 101 | 101 | 293 |
| 16 | 117 | 106 | 106 | 315a |
| 17 | 123 | 120 | 105 | 330 |
| 18 | 122 | 117 | 117 | 343 |
| 19 | 120 | 127 | 115 | 360 |
| 20 | 116 | 137 | 120 | 366 |
| 21 | 120 | 145 | 120 | 365 |
| Sacrals | | | | |
| 1 | 132 | 142 | — | 382 |
| 2 | 115 | 130 | — | 346 |
| 3 | 112 | 70 | — | 305 |
| 4 | 98a | 52 | — | 288 |
| 5 | 71a | 42 | — | 302 |
| 6 | 118 | 56 | — | 324 |
| 7 | 124 | 82 | — | 358 |
| Caudals | | | | |
| 1 | 128a | 140 | 126a | 346 |
| 2 | 122 | 144 | 118 | 341 |
| 3 | 120 | — | 120 | 326 |
| 4 | 136 | 104 | 117 | 324 |

a = approximate.

† = from dorsal border of epipophysis to posteroventral border of the centrum.

## APPENDICULAR SKELETON

### Pectoral Girdle and Forearm

**Scapulo-Coracoid and Sternal Plates.** Both scapulo-coracoids are completely preserved. The cor-

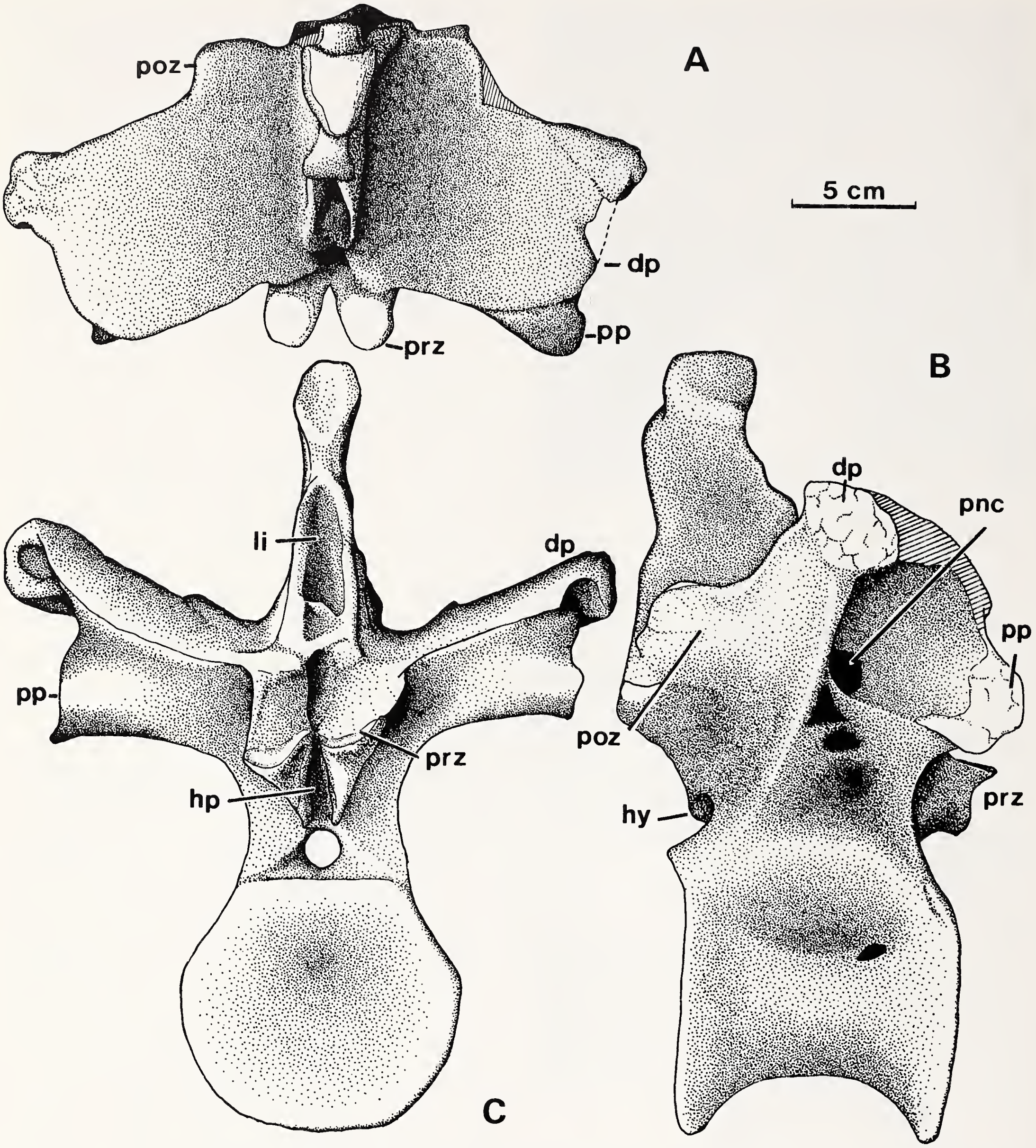

**Figure 19.** *Carnotaurus sastrei.* Tenth dorsal vertebra in dorsal (**A**), lateral (**B**), and anterior (**C**) views. Abbreviations as in previous figures.

acoid and the proximal part of the scapula are rather large compared with the modest scapular blade (Fig. 27). The latter has a constant width from a little above the glenoid cavity to the distal end, where there is no expansion as in *Tyrannosaurus* (Osborn, 1917) or other carnosaurs.

The anterior border of the scapula passes gradually to the acromial area, resembling the condition of *Deinonychus,* whereas it is more angular in *Tyrannosaurus, Allosaurus,* and *Ceratosaurus.*

The scapula and coracoid are strongly fused. The coracoid is large, with the distal border making a wide, continuous curvature, from near the posterolateral process of the coracoid up to the scapulo-coracoid suture on the anterior border. The position of the posterolateral process is near the glenoid cavity, a character we have not seen in other Carnosauria. In this area there are rugosities suggesting strong muscular attachment, probably of the m. biceps.

At the level of the glenoid cavity there is a large subacromial depression, located below a border of

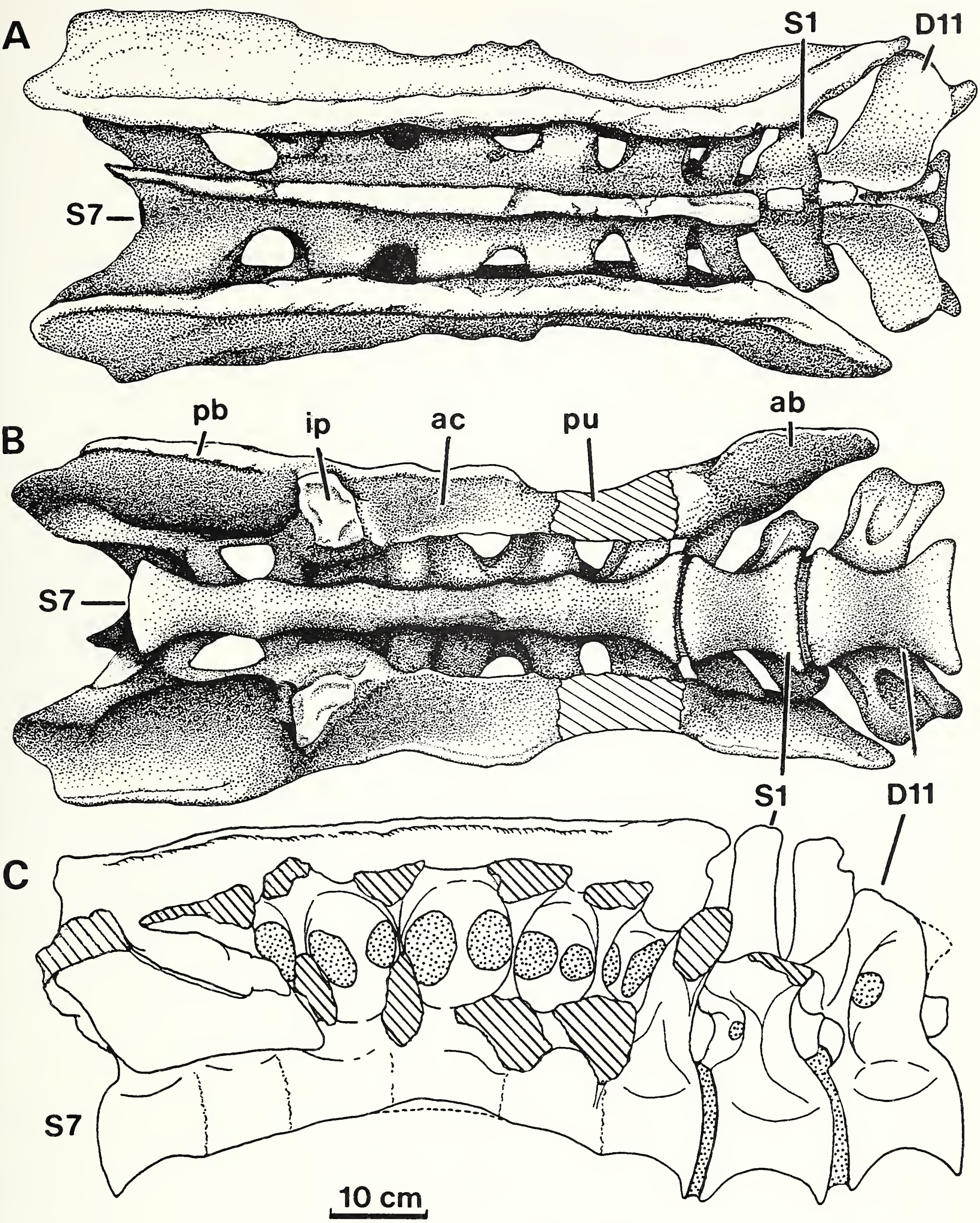

**Figure 20.** *Carnotaurus sastrei.* Sacrum and both ilia in dorsal (**A**), ventral (**B**), and lateral (**C**) views. ab, anterior blade; ac, acetabulum; D11, 11th dorsal vertebra; ip, ischiatic peduncle; pb, posterior blade; pu, pubic peduncle; S1 and S7, 1st and 7th sacral vertebra.

the scapula that may be the acromial process. The coracoid foramen is large and perforates the coracoid with a slight inclination.

The glenoid cavity is well defined, with well-developed supra- and infraglenoid processes that enlarge the articular region dorsally and ventrally. The shape is subspheric, except in the posterior section of the coracoid where the cavity between the processes is flat.

Near the area of the glenoid cavity in both scap-

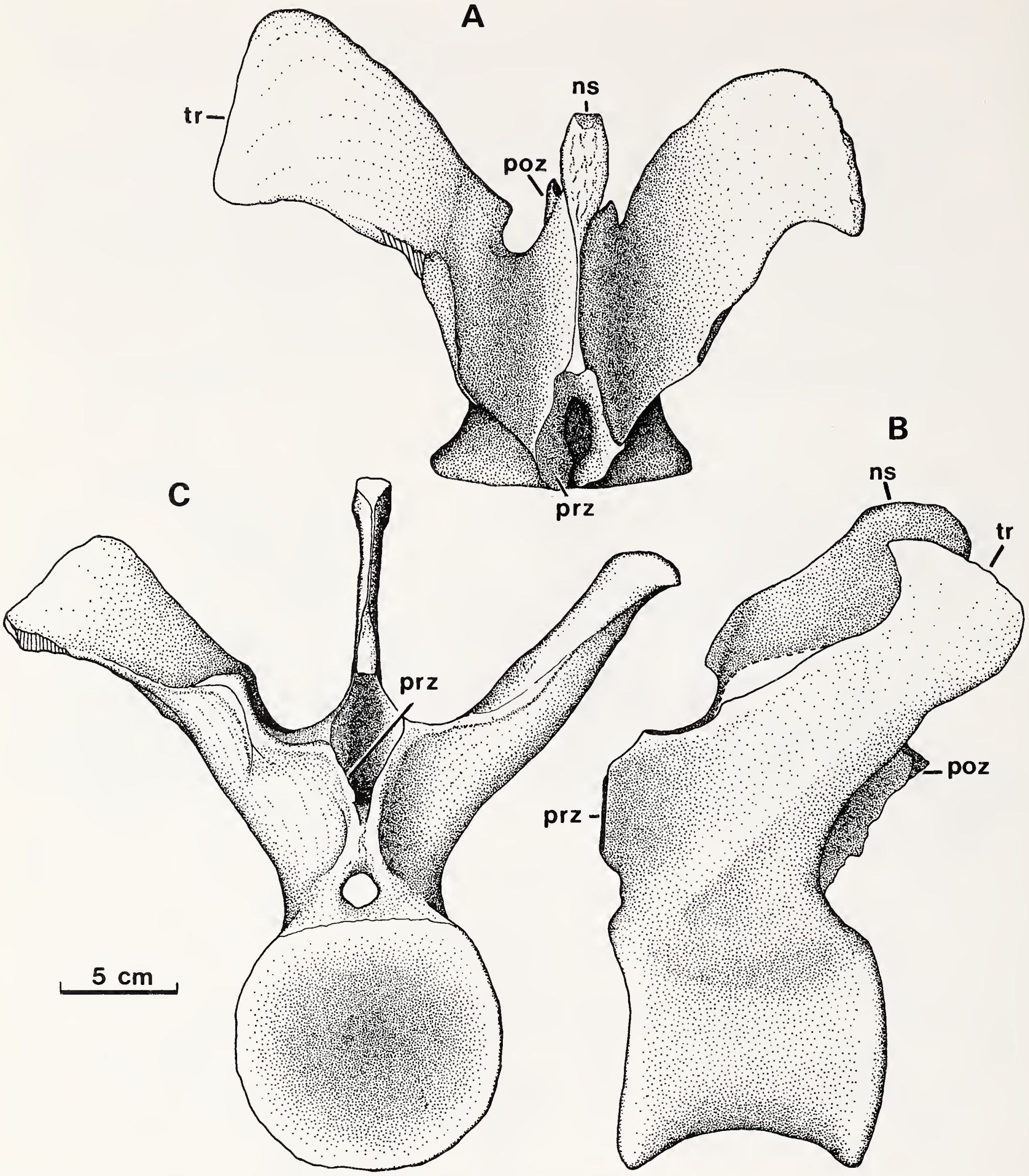

**Figure 21.** *Carnotaurus sastrei.* First caudal vertebra in dorsal (**A**), lateral (**B**), and anterior (**C**) views. Abbreviations as in previous figures, and: tr, transverse process.

ulo-coracoids there is an ossification on the inner side of the bones (about 50 mm in diameter), the function of which is unknown to us.

In life, the scapular blade was probably almost parallel with the row of dorsal vertebrae. On the internal side of the coracoid there are marks of dorsal ribs, indicating that they were parallel to the long axis of the coracoid.

The *clavicle* (Fig. 27C) may be represented by a slightly curved, rod-like bone with a modest, proximal expansion. It was lying on the anteroexternal portion of the right coracoid, in front of the sternal plates. Because of its position and morphology we interpret it as the right clavicle, although some portion of it may be missing.

The *sternal plates* (Fig. 27C) are preserved nearly complete. They were found close behind the coracoids. The right humerus was lying on the lateral surface of the right sternal plate. They are nearly flat and oval in outline, with a short ventral projection and two rib processes projecting posterodorsad and separated by a concavity.

The position of the sternal plates as found, *i.e.*, touching the medial border of the coracoids, may not have been too far from their natural position.

**Forelimbs**. The two forelimbs are almost complete, articulated, and with both humeri within the glenoid cavity. Unfortunately, the forefeet are not completely articulated, and some bones are not easy to interpret.

The forelimbs of *Carnotaurus* have significant derived characters, particularly in the epipodial bones, which are strongly reduced and appear to be a functional part of the hand. In this, the Patagonian genus shows derived characters not recorded in other Theropoda.

The *humerus* (Fig. 28) is robust and relatively short. Its dorsal region is transversely convex, and the internal side is concave proximodistally, as is common in the Carnosauria, and the opposed side is convex in the same direction. This means that in dorsal view the humerus is curved distally and internally, and in lateral view relatively straight.

The humeral head is well defined and subspheric, with similar length axes in the dorsoventral and lateromedial direction. A well-defined, but short, neck is present. These characters suggest that the humeral movements were pronounced in all directions, although the anteroposterior component was probably greater. The internal tuberosity is well developed, although proportionally smaller than in *Piatnitzkysaurus* (Bonaparte, 1986a) or *Allosaurus* (Madsen, 1976). The deltopectoral crest is massive, with the distal area most pronounced. Distally, the articulations for radius and ulna are dorsoventrally large and relatively flat, suggesting that the forelimb bones did not rotate on them significantly and that movements were probably restricted to the anteroposterior plane. Several typical characters of the theropod humerus have been strongly modified in the distal area of the *Carnotaurus* humerus: a) the large supracondyloid depression on the dorsal face was replaced by a convexity of the bone; b) the intercondylar depression on the ventral side was also modified, and this area is convex; c) the articular condyles were modified from subspheric to flat and dorsoventrally large; and d) the proximodistal torsion of the humerus is notably reduced.

The *radii* and *ulnae* (Figs. 29A–C, 30) are complete, and in articulation with the humeri and each other. They are very short, each only ¼ the length of the humerus. The ulna has a large, concave articular facet for the humerus, with the posterior area elevated and transversely wide. The anterior part of the facet is narrow and in a lower position than the posterior. In proximal view, the articular facet is triangular, with the apex anterior. The distal articulation is a wide condyle, convex in both directions, with the longest axis directed anteroposteriad. A marked neck lies between the distal articulation and the short diaphysis.

The radius is slightly shorter than the ulna. It has a large, rather flat, proximal articular facet. It articulates with the ulna via a convex area near its proximal end. The distal articulation is large and wide in both directions, but less convex than that of the ulna. There is not as great a difference between the size of the shaft and the ends of the bone as seen in the ulna. A well-defined osseous process, whose function is unknown, is found on the lateral side of the diaphysis and in the middle of its length.

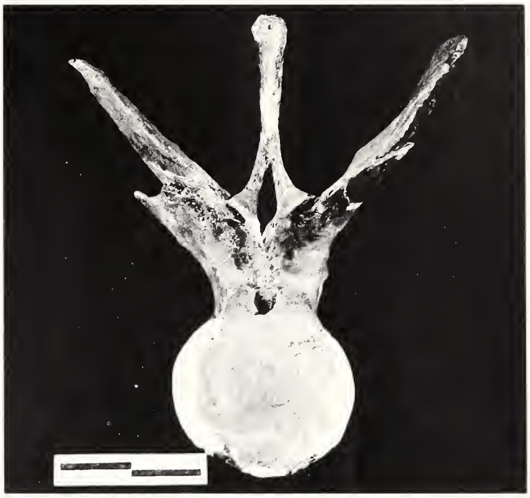

**Figure 22.** *Carnotaurus sastrei.* Second caudal vertebra in posterior view. Scale = 10 cm.

Large parts of both the right and left *manus* have been preserved, although we do not have a definitive interpretation of the distribution or relationship of the different pieces of their carpi and digits of the *Carnotaurus*. The reconstruction is tentative (Fig. 29C); however, we observe the following:

a) There is a group of carpal bones, of unknown number, below the ulna.

b) Four metacarpals are present. Metacarpal I is short, similar in length to metacarpal III; metacarpal II is the largest, morphologically similar to I, but ⅓ longer in size, with a large proximal articulation; metacarpal III is shorter than II, but transversely wider than metacarpals I and II, with the proximal area anteroposteriorly large and the distal area smaller; metacarpal IV is atypical, with a very large articulation for the large condyle of the ulna.

c) The first row of phalanges was limited to digits I, II, and perhaps III. The second row of phalanges is represented only by a proximal fragment of the second phalanx of digit II.

**Comparisons of Pectoral Girdle and Forelimb.** A comparison of the scapulo-coracoid of *Carnotaurus* with that of the genera of the families Allosauridae, Tyrannosauridae, and Ceratosauridae shows strong differences. The weakly developed acromial region of *Carnotaurus* differs greatly from that in the cited families, in which this region is well developed. Also, in *Carnotaurus* the posterolateral process of the coracoid is very near the glenoid cavity.

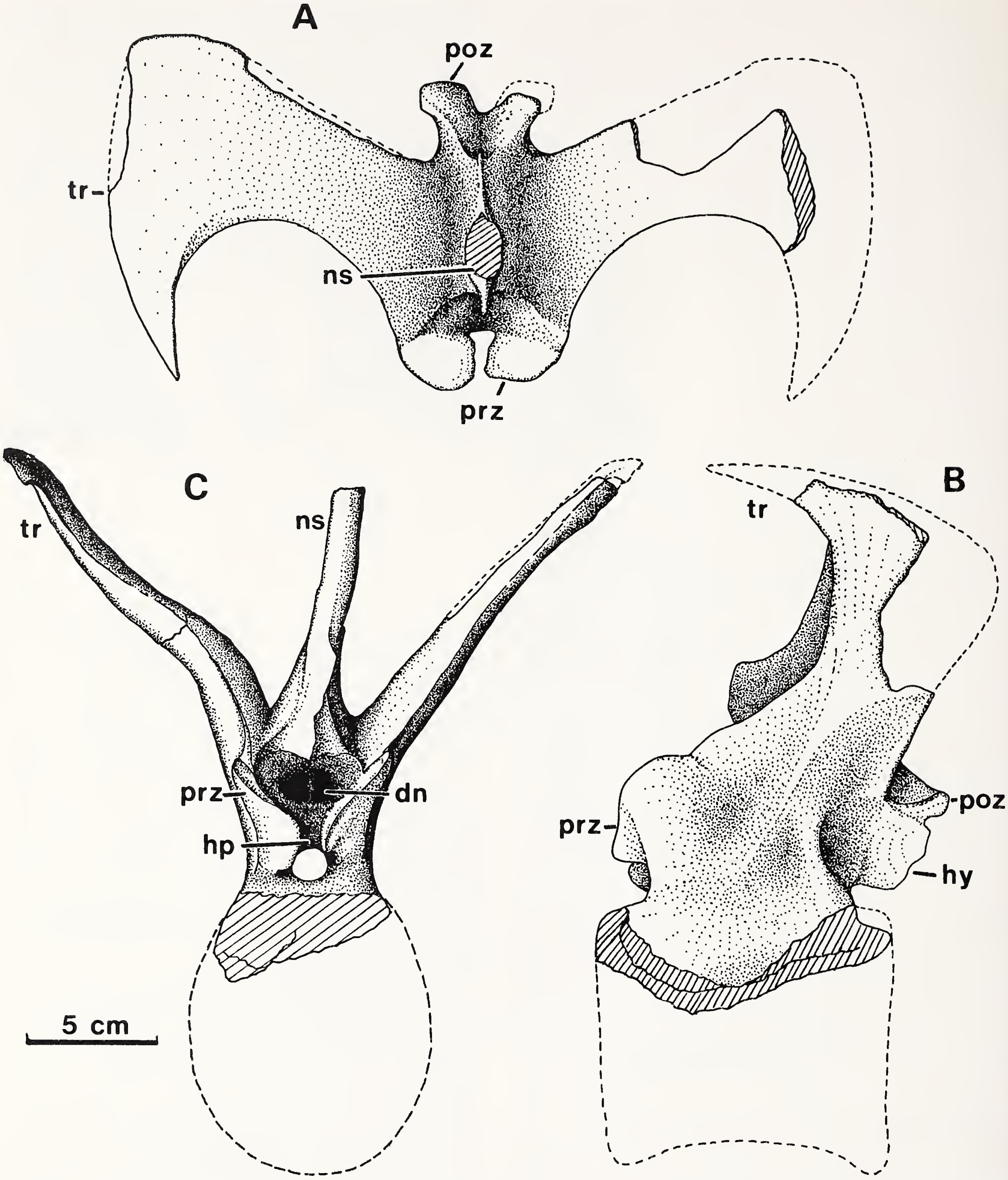

**Figure 23.** *Carnotaurus sastrei.* Neural arch and incomplete centrum of the 6th caudal vertebra in dorsal (**A**), lateral (**B**), and anterior (**C**) views. Abbreviations as in previous figures.

The scapular blade resembles more of the dromaeosaurid type of scapula, particularly that of *Deinonychus,* with the parallel anterior and posterior borders and the modest acromial expansion. However, differences with the coracoid of *Deinonychus* are strong enough to minimize any phylogenetic or systematic interpretations based on the similarities of the scapular blade.

The humerus of *Carnotaurus* is very similar to that of *Tyrannosaurus* (Osborn, 1917: fig. 21) and *Albertosaurus* (Lambe, 1917: fig. 31), although there are clearly differences in details, such as a more reduced deltopectoral crest, a more developed internal tuberosity, and a more derived distal region in the humerus of *Carnotaurus.*

The megalosaurid *Torvosaurus* (Galton and Jensen, 1979) has a different model of humerus with respect to *Carnotaurus* in the development of the deltopectoral crest and humeral head. *Carnotaurus* has radii and ulnae proportionally shorter than *Torvosaurus.*

In the manus, the morphology and proportion of the several bones observed, and the characters of the distal end of the radius and ulna, are not typical for a carnosaur. The hand shows a group of plesiomorphic (*e.g.*, four digits) and apomorphic (*e.g.*, metacarpal IV with a very large articulation for the distal condyle of the ulna) characters, whose association has not been reported in other Theropoda, except in *Ceratosaurus* where Gilmore (1920: figs. 60, 62) illustrated four digits with short phalanges.

We believe that the strong modification in the forelimbs of *Carnotaurus,* among them the almost total lack of torsion of the humerus and the parallel position of radius and ulna, resulted in a complete

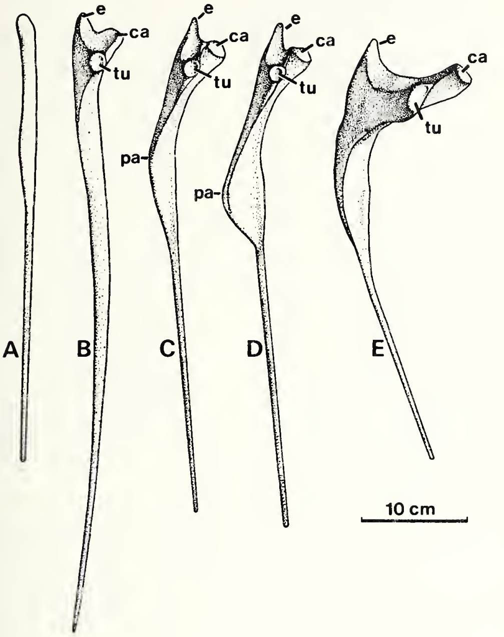

**Figure 24.** *Carnotaurus sastrei.* Left cervical ribs: 1st (**A**), 3rd (**B**), 4th (**C**), and 5th (**D**) in dorsal view and 8th (**E**) in dorsomedial view. ca, capitulum; e, anterior spine; pa, aliform process; tu, tuberculum.

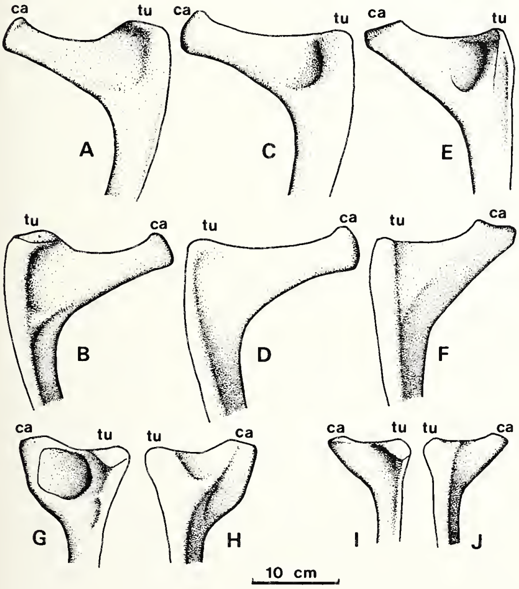

**Figure 25.** *Carnotaurus sastrei.* Proximal ends of right dorsal ribs. 1st rib (**A, B**), 2nd rib (**C, D**), 4th rib (**E, F**), 9th rib, (**G, H**), 11th rib (**I, J**) in ventral (A, C, E, G, I) and dorsal (B, D, F, H, J) views.

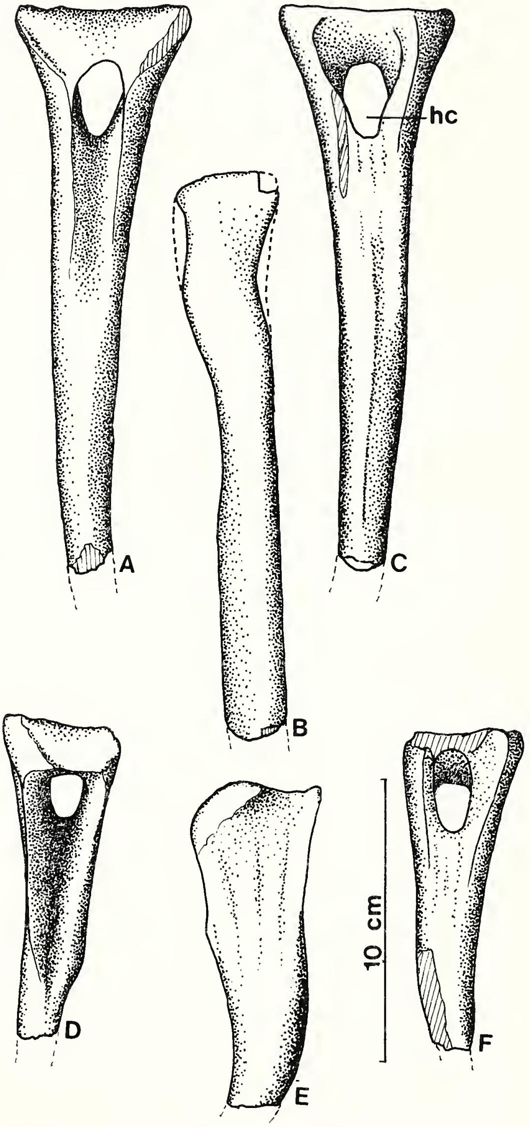

**Figure 26.** *Carnotaurus sastrei.* Fourth haemal arch (**A–C**) and 10th haemal arch (**D–F**) in dorsal (A, D), lateral (B, E), and ventral (C, F) views. hc, haemal canal.

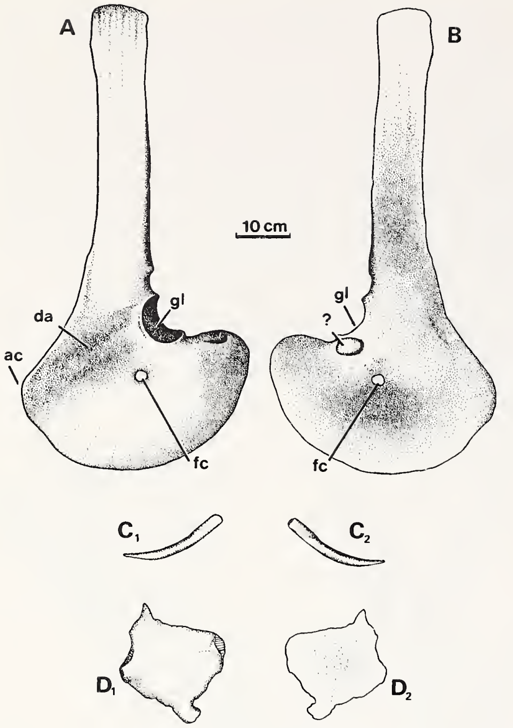

**Figure 27.** *Carnotaurus sastrei.* Left scapulo-coracoid in lateral (**A**) and medial (**B**) views. Right clavicle in lateral (C1) and medial (C2) views. Sternal plate in lateral (D1) and medial (D2) views. ac, acromium; da, subacromial depression; fc, coracoidal foramen; gl, glenoid cavity; ?, indeterminate ossification.

change of the original position of the hand. If this is true, the palmar side moved to a dorsal position, with digit I assuming a lateral position and digit IV an internal position.

**Table 3. Measurements (in millimeters) of the shoulder girdle of *Carnotaurus sastrei.***

| | Right | Left |
|---|---|---|
| Greatest length of scapula and coracoid measured along curve of outside | 905 | 900 |
| Maximum length of scapula | 645 | 610 |
| Maximum breadth of scapular blade (at level of tubercule for *m. triceps*) | 128 | 133 |
| Greatest transverse expanse of glenoid fossa | 63 | 70 |
| Greatest proximodistal expanse of glenoid fossa | 80 | 95 |
| Greatest length of coracoid | 430a | 430a |
| Greatest depth of coracoid | 290 | 290 |
| Anteroposterior expanse of sternal plate | 180 | — |

a = approximate.

**Table 4. Measurements (in millimeters) of the forelimb and manus of *Carnotaurus sastrei.***

| | Right | Left |
|---|---|---|
| Humerus | | |
| Length | 285 | 284 |
| Distal transverse width | 86 | 93 |
| Proximal transverse width | 95 | 100 |
| Transverse width of humeral head | 76 | 75 |
| Anteroposterior width of humeral head | 70 | 73 |
| Least transverse width of shaft | 53 | 55 |
| Ulna | | |
| Length | 78 | 85 |
| Greatest distal transverse width | 59 | 55 |
| Greatest proximal transverse width | 50 | 56 |
| Greatest anteroposterior distance of proximal end | 66 | 71 |
| Least diameter of shaft | 22 | 26 |
| Radius | | |
| Length | 73 | 80 |
| Greatest distal transverse width | 63 | 58 |
| Greatest proximal transverse width | 47 | 48 |
| Least diameter of shaft | 30 | 31 |
| Radiale | | |
| Length (proximodistal) | 10 | — |
| Transverse width | 25 | — |
| Ulnare | | |
| Length | 18 | — |
| Transverse width | 24 | — |
| Metacarpal I | | |
| Length | 30 | — |
| Proximal transverse width | 23 | — |
| Distal transverse width | 23 | — |
| Metacarpal II | | |
| Length | 37 | 36 |
| Proximal transverse width | — | — |
| Distal transverse width | 23 | — |
| Metacarpal III | | |
| Length | 29 | 31 |
| Proximal transverse width | — | — |
| Distal transverse width | — | — |
| Metacarpal IV | | |
| Length | 84 | — |

## Pelvic Girdle and Hindlimb

The pelvic bones were articulated to each other, the sacrum, and the femora. The farmer who found the specimen, Mr. Sastre, removed some marginal rock containing the distal part of both ischia. The length of the ischium (Fig. 31) is, therefore, an estimate, and a few centimeters could possibly be added between the preserved parts.

**Pelvic Girdle** (Fig. 31). The ventral bones of the

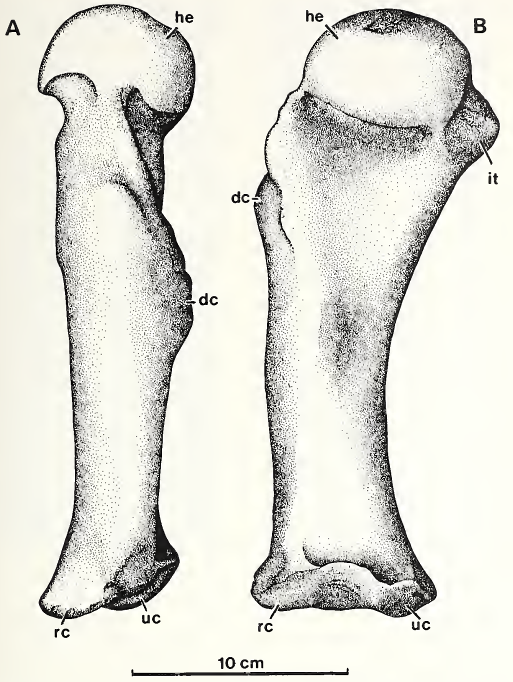

Figure 28. *Carnotaurus sastrei.* Right humerus in lateral (**A**) and anterior (**B**) views. dc, deltopectoral crest; he, humeral head; it, internal tuberosity; rc, radial condyle; uc, ulnar condyle.

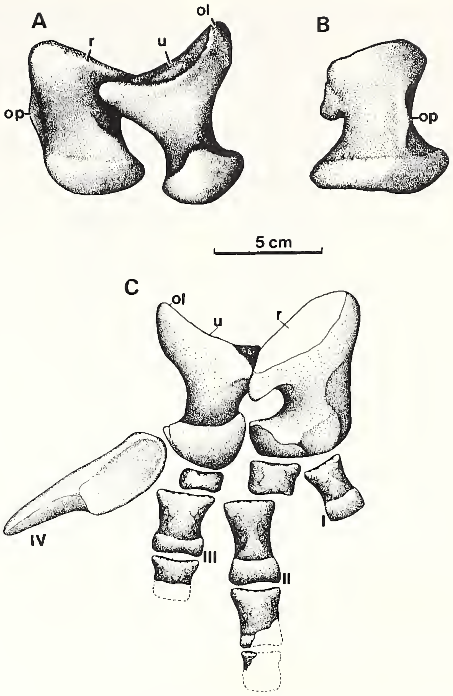

Figure 29. *Carnotaurus sastrei.* Right radius and ulna in anterolateral view (**A**), right radius in medial view (**B**), and right radius and ulna with tentative reconstruction of right manus in palmar view (**C**). ol, olecranon; op, osseous process; r, radius; u, ulna; I, II, III, IV, metacarpals I, II, III, and IV.

*Carnotaurus* pelvis are proportionately long, slender, and straight, and the distal end of the ischium is expanded into a foot. The acetabulum is large and open medially, and all three pelvic bones contribute to it.

The *ilium* (Figs. 20, 31) is long and low, with the dorsal border rounded and axially straight, except its anterior area where it bends ventrad. The ventral border behind the acetabulum is parallel with the dorsal border. The iliac blade has a high posterior border and is concave in its central area. The anterior projection of the ilium is dorsoventrally large, and it projects ventrad more than in *Tyrannosaurus* (Osborn, 1917) or *Allosaurus* (Madsen, 1976), resembling the condition of *Ceratosaurus* (Gilmore, 1920).

The precise union between the pubis and the ilium is hard to locate. A series of rugosities may correspond to that union, as tentatively indicated in Figure 31. The pubic pedicel is wide and short.

The *pubis* (Fig. 31) has a large contact with the ischium, and the obturator foramen is largely encircled by bone. The shaft is almost straight, with a well-developed foot and a long, fused symphysis. Proximal to the distal foot, both pubes are separated by an elongate aperture.

The *ischium* (Fig. 31) is long and proportionally thicker than the pubis. Both ischia are fused for most of their length. Ventrally, the fused area is present from the distal end up to the middle of the ventral laminae. Dorsally, the fused area is shorter, and before the level of the ventral laminae is reached distad, both ischia begin to separate along their dorsal edge. Proximally, the ventral laminae are separated and form a wide acetabular concavity. The union with the pubis is laminar via a strong fusion. The posterior pedicel of the ilium shows a partial fusion with the ischium. In the proximolateral region, almost on its dorsal border, there is an obvious osseous process for muscular attachment, possibly for the *m. flexor tibialis internus.* According to Gregory and Camp (1918) this is a character present in *Ceratosaurus* and *Tyrannosaurus,* but not in *Allosaurus* or *Deinonychus.*

In the distal area the ischia are intimately fused and show an anteroposterior, foot-like expansion. As the distal portions of the ischia are not in clear contact with the proximal portions, as indicated above, we do not know the actual length of these bones.

**Hindlimb** (Figs. 32, 33). The hindlimbs are represented only by the femora and the proximal third of both tibiae. Unfortunately, erosion destroyed the rest of both hindlimbs, including the feet. However, there is sufficient information from other re-

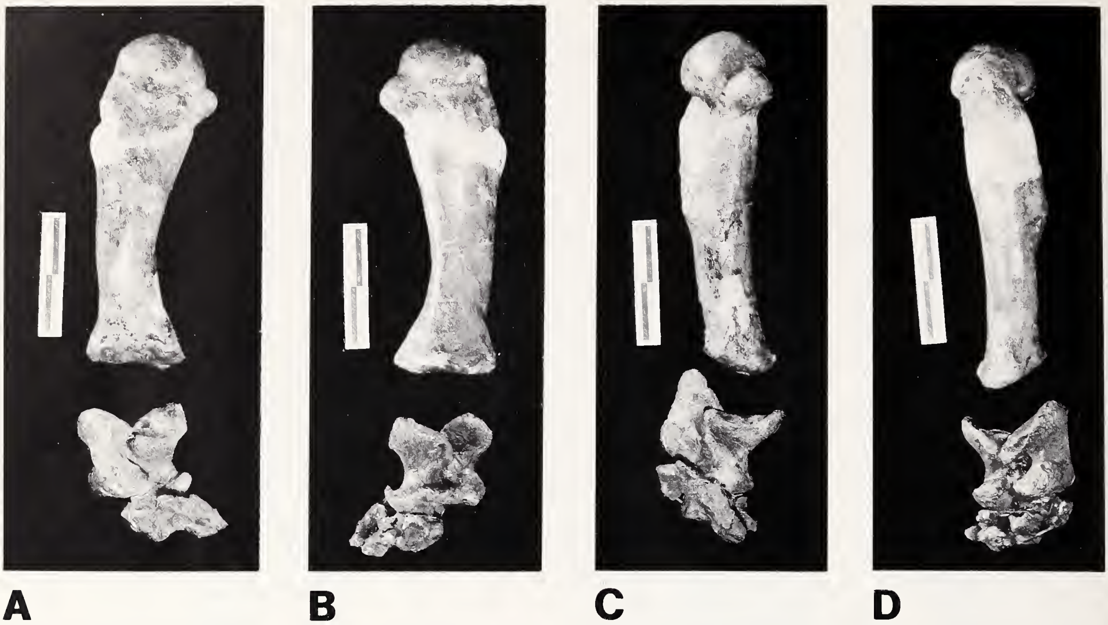

**Figure 30.** *Carnotaurus sastrei.* Right humerus, radius, and ulna in anterior (**A**), posterior (**B**), medial (**C**), and lateral (**D**) views. Scale = 10 cm.

cent finds made in Patagonia that permits restoration of the hindlimbs, except for the tarsals and digits.

In general terms, *Carnotaurus* had long and slender hindlimbs, not very different from those of *Bahariasaurus* (Stromer, 1915). They show both primitive and derived characters that distinguish them from *Tyrannosaurus* and, to a lesser degree, from *Allosaurus.*

The left *femur* (Fig. 32) is reasonably complete, with the central portion restored after a natural mold. Its total length is 103 cm, and the average diameter of the diaphysis is 11 cm, a good indication of its slender condition. D. Russell (pers. comm.) suggests that the size of the femur indicates that the total weight of this *Carnotaurus sastrei* specimen was about 1,350 kg.

The distal end of the femur has a modest transverse expansion, to 19 cm, and the proximal end has a length to the major anteromedial axis of 22 cm. The diaphysis is subcylindrical and proximodistally convex on the anterior side. In the distal internal region, a sharp mediodistal crest originates and ends near the inner tibial condyle. This crest separates the concave dorsal surface from the medial side, which is also concave. The inner tibial condyle projects strongly posteriad, but it is transversely narrow, whereas the outer condyle is transversely wider but less pronounced posteriorly. The major axis of the fibular condyle projects upward and outward.

At the proximal end the femoral head has a convex continuity with the major trochanter. The femoral head is, therefore, anteroposteriorly narrow and not subspheric as in *Tyrannosaurus.* Nor does it project mediad as in *Tyrannosaurus* and *Allosaurus,* but instead it projects anteromediad. The lesser trochanter is well developed, but proximally

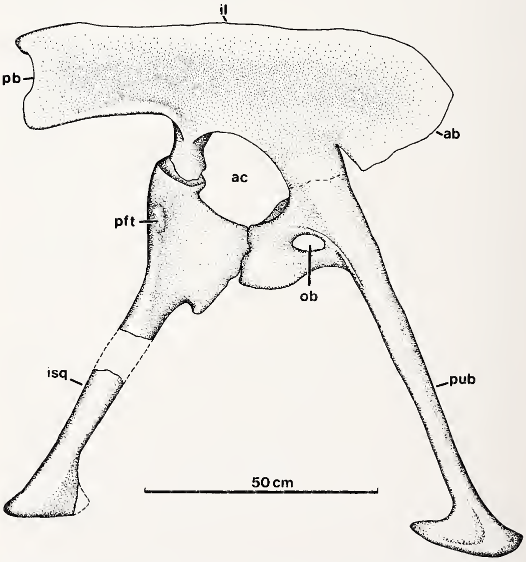

**Figure 31.** *Carnotaurus sastrei.* Pelvis in lateral view. Ilio-pubic suture suggested by dashed line. ab, anterior blade; ac, acetabulum; il, ilium; isq, ischium; ob, obturator foramen; pb, posterior blade; pft, process for the *m. flexor tibialis internus;* pub, pubis.

**Table 5.** Measurements of pelvic bones and hindlimb of *Carnotaurus sastrei.*

| | |
|---|---|
| Ilium | |
| Greatest length | 970 |
| Height above middle of acetabulum | 235 |
| Ischium | |
| Greatest expanse from ventral border of obturator process to posterior border of iliac pedicel | 250 |
| Pubis | |
| Greatest length along anterior border | 880 |
| Greatest length of distal "foot" | 252 |
| Greatest length of distal "foot" | 106 |
| Greatest transverse width at center of combined shaft of both pubes | 157 |

| | Right | Left |
|---|---|---|
| Femur | | |
| Greatest length | — | 1030 |
| Greatest diameter of head | — | 206 |
| Distal width | 197 | 198 |
| Tibia | | |
| Proximal width | 120 | 134 |
| Greatest anteroposterior expanse | 245a | 245a |

a = approximate.

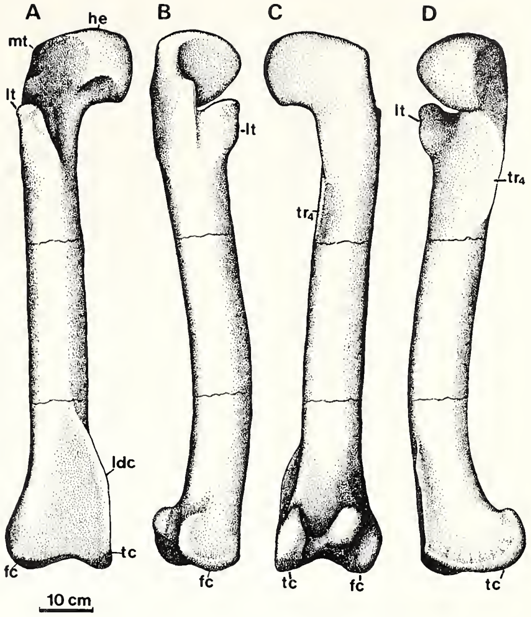

**Figure 32.** *Carnotaurus sastrei.* Right femur in anterior (**A**), lateral (**B**), posterior (**C**), and medial (**D**) views. fc, fibular condyle; he, femoral head; ldc, mediodistal crest; lt, lesser trochanter; mt, major trochanter; tc, tibial condyle; tr4, 4th trochanter.

it reaches to only slightly below the femoral head. Both *Tyrannosaurus* and *Allosaurus* have dorsally higher lesser trochanters. The internal, or 4th, trochanter is not well preserved, but its relative position appears to be somewhat higher than in *Tyrannosaurus.*

The *tibiae* (Fig. 33A, B) are represented only by their proximal parts. The articular surface for the femur is inclined outward and downward. The outer facet is in a posterior position, near the posterior border of the tibia. The articulation for the fibula is anteroposteriorly convex. The cnemial crest is not complete, but it appears to have been well developed, although perhaps less so than in *Allosaurus.* The crest for a ligamentous union with the fibula is dorsally placed, and it lies slightly anterior to the fibular condyle.

**Reconstruction of Tibia-Fibula-Tarsus of *Carnotaurus.*** Recently, some associated remains of Carnosauria were described by Martínez *et al.* (1986). The material includes incomplete vertebrae and a complete femur, tibia, fibula, and tarsus, on which *Xenotarsosaurus bonapartei* Martínez, Giménez, Rodríguez, and Bochatey from the Upper Cretaceous of Patagonia was based.

The similarities of the preserved vertebrae and limb bones of this theropod with those of *Carnotaurus* are so marked that its familial indentification is unquestionable, as Martínez *et al.* (1986) recognized. The generic differences are based on the vertebral morphology, where some differences exist. But the morphology of the femora strongly suggests that the hindlimbs of both forms were probably basically the same.

On this basis we estimate that the tibiae of *Carnotaurus* were slightly shorter than the femora, possibly about 97 cm in length. It is possible that the distal region of the tibia had a moderate transverse expansion and that it might have been fused to the astragalus and calcaneum, as in *Xenotarsosaurus,* forming a rigid unit. The fibula was probably not fused to its neighboring bones, as in *Xenotarsosaurus.*

**Comparisons of Pelvic Girdle and Hindlimb.** The pelvis of *Carnotaurus* is typically carnosaurian, with similarities to *Ceratosaurus nasicornis.* We see little indication of phylogenetic affinities with Deinonychosauria or Coelurosauria. There are strong differences in the morphology of the tyrannosaurid ischia, which lack a distal expansion, and the tyrannosaurid pubis, which is transversely wide and robust and lacks an obturator foramen.

The general plan of the sacrum and pelvis is comparable to that of *Ceratosaurus,* with an axially extended ilium, an elongated, slender pubis with an obturator fenestra encircled by bone, and a wide, laminar contact between the pubis and ischium. The ischium is elongated and rather slender, and it has a distal foot-like expansion in both genera (Marsh, 1896: pl. 10, fig. 1; Gilmore, 1920: 108). *Carnotaurus* shows derived characters, relative to

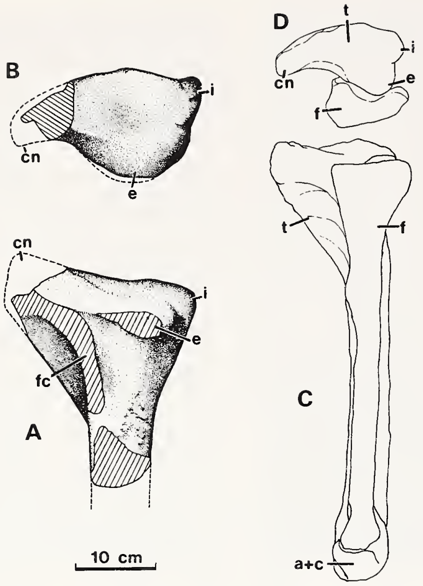

**Figure 33.** *Carnotaurus sastrei.* Proximal end of the left tibia in lateral (**A**) and proximal (**B**) views, compared with the left tibia, fibula, and tarsus of *Xenotarsosaurus bonapartei* in lateral (**C**) and proximal (**D**) views. a+c, astragalus and calcaneum; cn, cnemial crest; e, external condyle; f, fibula; fc, fibular crest; i, internal condyle; t, tibia.

*Ceratosaurus,* in having the dorsal border of the ilium straight and parallel to the ventral postacetabular border, which forms a right angle with the high posterior border of the ilium, and in having the pubo-ischiatic symphysis more reduced. We believe the similarities are sufficient to consider the two genera to be closely related.

The hindlimb of *Carnotaurus* has very slender proportions, which suggests that it may have been a more agile form than other carnosaurs, except for the African forms described as *Bahariasaurus* and cf. *Spinosaurus* (Stromer, 1934: pls. 1, 3). However, the hindlimb shows significant plesiomorphic characters relative to *Allosaurus* and *Tyrannosaurus,* including a) femoral head projecting anteromediad; b) femoral head slightly lower than the major trochanter, with a convexity between them; and c) lesser trochanter with a modest dorsal projection. These differences suggest that the Allosauridae and Tyrannosauridae are quite distinct from the Abelisauridae, which includes *Carnotaurus.*

The *Ceratosaurus* femur (Gilmore, 1920: fig. 64) is similar to *Carnotaurus* in the following features: a) morphology and relative position of the femoral head and the major trochanter; b) characters of the lesser trochanter in its dorsal expression; c) characters of the distal end, including the relative position and morphology of the tibial and fibular condyles; and d) the position and characters of the anteromedial crest that separate the medial from the anterior face of the dorsal side in this part of the femur.

The similarities with the African Cenomanian forms (Stromer, 1915, 1931, 1934) are significant, but some differences are present. The region of the femoral head-major trochanter is the same, but the lesser trochanter is more developed. In the distal end of the femur there are several peculiar characters in the African forms. In the proximal end of the tibia, the fibular condyle is not near the posterior border as in *Carnotaurus,* but rather it is in a more anterior position.

### Skin

Several fragments of skin impressions were found underneath the right side of the skeleton. They correspond to several parts of the body. One fragment is from the anterior cervical region, and it is associated with the anterior cervical ribs. Another fragment is from the scapular area near the glenoid cavity. Two fragments are from the thoracic region, and they are associated with the mid-proximal area of the ribs. The largest available skin impression corresponds to the lower area of the proximal part of the tail. There appears to be little variation among the different fragments. The surface of the skin is made of rather low, conical protuberances of about 4 to 5 cm in diameter (Fig. 37), each with a modest keel and separated from one another by about 8 to 10 cm. The surface between the protuberances is rough, with rather rounded, low, and small granules about 5 mm in diameter that are separated from one another by narrow furrows.

## GENERAL COMPARISONS

We consider *Carnotaurus sastrei* to represent a new, previously unknown adaptative type within the Theropoda that has many derived skeletal characters. These derived characters may give us a wider perspective of the adaptive potentialities of this group of dinosaurs, and we believe that the unique anatomical characters of *Carnotaurus* must be considered in developing the systematics of the Carnosauria.

It is necessary, perhaps, to overcome an interpretation of the 1970's in which the biogeography of the Gondwana dinosaurs was only superficially considered, *e.g.,* Charig (1973: 351): ". . . it may be that the congeneric dinosaurs found in the various Gondwanaland regions (if indeed congeneric) were merely the remnants of populations, once widely distributed, which have been driven south by various agencies into the already isolated peninsulas of the Southern Hemisphere." The biogeographic history of the Cretaceous dinosaurs of Gondwana was probably completely different from that implied by Charig's statement.

### Is *Carnotaurus sastrei* a Carnosaur?

Typical members of the Carnosauria are represented by the Jurassic and Cretaceous families Megalosauridae, Allosauridae, Ceratosauridae, and Tyrannosauridae. In addition, the families Dryptosauridae, Spinosauridae, and Abelisauridae are very probably members of the Carnosauria. All of these families represent a relatively homogeneous group of predators of considerable size, in which a progressive reduction of the forelimbs is documented. These families are also characterized by long pubes with a distal foot and with femora slightly longer than the corresponding tibiae. These characters, in association with other more generalized ones of the skull, ilium, scapulo-coracoid, and foot, distinguish the different taxa of the Carnosauria.

The inclusion of *Carnotaurus sastrei* among the Carnosauria is fairly conclusive because the outstanding reduction of the forelimbs, with the strong humerus, and the characters of the sacrum, pelvis, and femur point to a relationship with *Ceratosaurus.* All of these arguments clearly demonstrate that it is a carnosaur with several derived characters. We do not believe it is necessary to make comparisons with other groups of the Theropoda such as Deinonychosauria, Oviraptosauria, Ornithomimosauria, Segnosauria, and Therezinosauridae (*fide* Russell, 1984).

## Comparison with Jurassic and Cretaceous Carnosaurs of South America

All of the significant specimens of South American carnosaurs are from Argentina. The known remains from Brasil (Price, 1960) are isolated teeth. Likewise, taxa described by del Corro (1966, 1974) as *Megalosaurus inexpectatus* and *Megalosaurus chubutensis* lack diagnostic characters and should be considered as *nomina dubia.*

*Piatnitzkysaurus floresi* Bonaparte (1979, 1986a) is an allosaurid from the Middle Jurassic, Callovian, of Patagonia, showing some plesiomorphic characters relative to *Allosaurus fragilis.* The comparison of *Carnotaurus* with the Middle Jurassic form does not provide more information than the comparison with *Allosaurus.* However, the more primitive condition of *Piatnitzkysaurus* suggests that it is nearer to the common ancestry of Ceratosauridae-Abelisauridae than is *Allosaurus.*

*Genyodectes serus* Smith-Woodward, 1901, is based on the anterior part of a skull and jaws, and these show significant similarities with *Carnotaurus.* However, it lacks sufficient diagnostic characters to identify it with, or differentiate it from, *C. sastrei.* In addition, the geographic and stratigraphic provenance of *Genyodectes serus* is so imprecise that we are unable to determine if the type specimen came from Jurassic or Cretaceous deposits, much less from Middle or Upper Cretaceous deposits. We do not have the necessary stratigraphic or anatomical data for comparison. There is some doubt as to the validity of the taxon *Genyodectes serus.*

*Unquillosaurus ceibalii* Powell (1979) is based on most of a left pubis, bearing a "foot" and an anterolateral proximal canal. The obturator foramen is open, which is more derived than in *Carnotaurus sastrei.* Although *Unquillosaurus ceibalii* is based on incomplete material, there are sufficient differences to distinguish it from *Carnotaurus.*

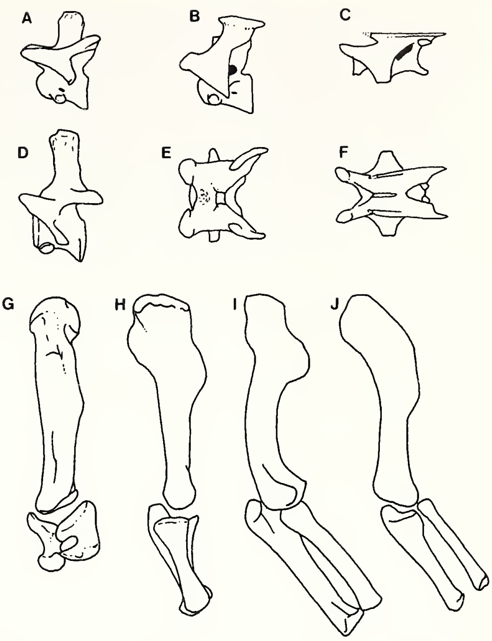

**Figure 34.** *Carnotaurus* 6th cervical vertebra (**B, E**), compared with those of *Allosaurus* (**A**) and *Ceratosaurus* (**D**), and with the neural arch of the cervical vertebra of *Noasaurus* (**C, F**); and humerus, radius, and ulna (**G**), compared with those of *Torvosaurus* (**H**), *Allosaurus* (**I**), and *Daspletosaurus* (**J**) in lateral view. Not to scale.

*Xenotarsosaurus bonapartei* (Martínez *et al.* 1986) is from the Bajo Barreal Formation, southern Chubut Province, Patagonia, probably Senonian in age. This species is based on two incomplete vertebrae associated with the femur, tibia, and tarsus of the right side. Martínez *et al.* (1986) recognized some significant differences between *Xenotarsosaurus* and *Carnotaurus* vertebrae as the depressions of the vertebral centrae are more marked, the parapophyses are larger, and the cavities underneath the prezygapophysis are more developed in *Xenotarsosaurus.* These characters suggest *Xenotarsosaurus* is a distinct genus.

A comparison of what is preserved of the hindlimb of *Carnotaurus* with the limb bones of *Xenotarsosaurus* is very useful, the similarities showing that both genera are in the same family. Characters of the femora of both genera are similar, except that the *Carnotaurus* femur is relatively longer and more slender. A comparison of the proximal part of the tibiae shows common characters in the posterior position of the external tibial condyle, the morphology of the cnemial crest, and the relative position of the fibular crest. *Xenotarsosaurus* shows some differences from *Carnotaurus* in the verte-

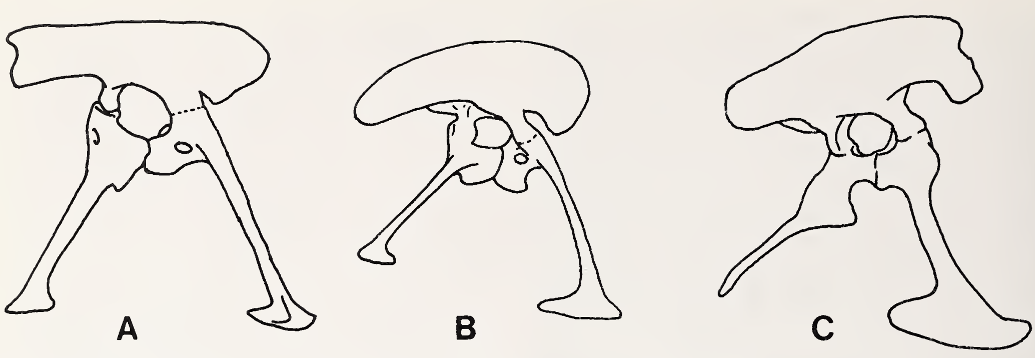

**Figure 35.** *Carnotaurus* pelvis (**A**) compared with that of *Ceratosaurus* (**B**) and *Tyrannosaurus* (**C**) in lateral view. Not to scale.

brae, but the characteristics of the hindlimbs show that both genera belong to the Abelisauridae.

*Abelisaurus comahuensis* Bonaparte and Novas, 1985, is based on an incomplete skull from the Allen Formation, Maastrichtian, of Río Negro province, Patagonia. Even though the proportions of the skull are very different from the short, high skull of *Carnotaurus,* the two genera share several diagnostic features at the family level. In the temporal region of *Abelisaurus,* plesiomorphic characters exist in the squamosal and the general shape of the infratemporal opening. In the orbit, the postorbital almost encloses the orbit ventrally, and the lachrymal is posteriorly convex, as in *Carnotaurus.* The preorbital opening is large, but with different proportions than that of *Carnotaurus.* The position and small size of the maxillary fenestra, which is slightly separated from the main preorbital opening but is still within the same general depression, is similar in both genera. In the supratemporal region of both genera there are shared characters in the parietal crest and in the proportions of the openings. Finally, the ornamentation of the nasals with rugosities suggests a corneous covering in both genera. Although *Abelisaurus,* with its elongated skull, represents an adaptive type different from *Carnotaurus,* it is evident that they correspond to the same family.

*Noasaurus leali* Bonaparte and Powell, 1980, is a small theropod represented by only a few, but diagnostic, pieces from the Lecho Formation, Maastrichtian, of Salta Province, northwestern Argentina. The authors recognized a different family, Noasauridae, which, with some doubt, they referred to the Coelurosauria. Considering what is presently known of the anatomy of *Abelisaurus* and *Carnotaurus,* the original systematic interpretation may be subject to change.

The maxilla of *Noasaurus* (Fig. 7H) is relatively short and high, suggesting that the general shape of the skull was probably short. The preorbital opening resembles the condition in *Abelisaurus* and *Carnotaurus.*

The squamosal of *Noasaurus* (Fig. 7I) has a ventral process without a forward inclination. In this character it resembles *Abelisaurus* and *Carnotaurus,* although there are significant differences in other characters of the bone. The quadrate of *Noasaurus* (Fig. 7G) is long, in agreement with *Abelisaurus* and *Carnotaurus.*

The neural arch of the cervical vertebra of *Noasaurus* (Fig. 34C, F) shows characters similar to those of *Carnotaurus* (Fig. 34B, E). The outstanding development of the epipophysis and the reduced neural spine, which was assumed to be lacking by Bonaparte and Powell (1980), correspond to characters of the peculiar type of cervical neural arch of *Carnotaurus.* The cervical ribs of *Noasaurus* are very different from those of *Carnotaurus.*

Fundamental characters of the maxilla, squamosal, and quadrate, and especially the structure of the cervical neural arch of *Noasaurus* and *Carnotaurus,* suggest that although the two genera represent different families, they may belong to a common major taxon, possibly a superfamily.

### Comparisons with Tyrannosauridae

The comparisons with this family of Carnosauria are primarily made with *Tyrannosaurus* because it is generally considered very representative of the family.

The design of the *Tyrannosaurus* skull (Fig. 7K, L, M) corresponds to a long, low model, with a massive lower jaw in lateral view, with a reduced mandibular fenestra. *Carnotaurus* has a short, high skull, and the lower jaw is slender with a large mandibular fenestra. The significant differences of the infratemporal opening, orbital and preorbital region, characters of the jugal, lachrymal, and other bones have been pointed out in the description.

The general anatomy of the vertebrae posterior to the axis shows fundamental differences from that of *Tyrannosaurus* because of the hypertrophy of the epipophysis and atrophy of the neural spines in *Carnotaurus,* which are derived characters not

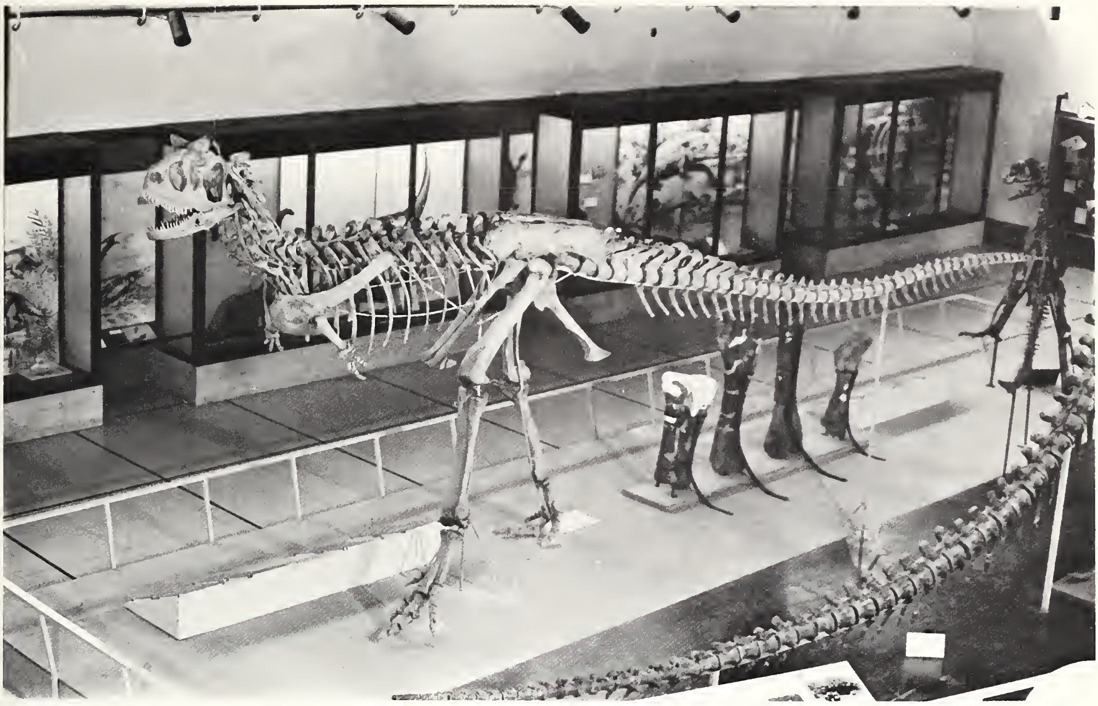

**Figure 36.** *Carnotaurus sastrei.* Cast of the skeleton at the Museo Argentino de Ciencias Naturales "B. Rivadavia," Buenos Aires, mounted in 1986.

present within the Tyrannosauridae. The forelimb shows derived characters in the outstanding reduction of the forearm and the degree of humeral torsion, characters different from those found in Tyrannosauridae (Fig. 34J). In the manus, the general plan of the digits is quite different in *Carnotaurus* and tyrannosaurids. In the pelvic girdle (Fig. 35), strong differences are seen in the morphology of the pubis and ischium, as the obturator foramen is encircled by bone and the ischium is expanded distally in *Carnotaurus.* In the hindlimb, the femur of *Carnotaurus* is relatively longer and more slender, the femoral head is medioanteriorly rather than medially projected, the lesser trochanter has a lower position, the 4th trochanter is more dorsally placed, and the fibular condyle has a different orientation.

The indicated differences between *Carnotaurus* and members of Tyrannosauridae make it clear that *Carnotaurus* does not belong to this family. The differences between Tyrannosauridae and Abelisauridae are actually more obvious and better defined than between the Tyrannosauridae and the other families of Carnosauria (Allosauridae, Megalosauridae, and Ceratosauridae).

### Comparison with Allosauridae

The differences between *Allosaurus* and *Carnotaurus* are significant and present throughout the skeleton. In general terms we may consider *Allosaurus* as a potential ancestor to the Tyrannosauridae because of several derived characters that persist or are more fully developed in the Cretaceous family (*i.e.*, the anteroventral projection of the squamosal, the short quadrate, the near absence of mandibular fenestra, the medial projection of the femoral head, and the well-developed pubis). None of these characters are typical of *Carnotaurus,* in which the plesiomorphic condition prevails. *Carnotaurus* has several apomorphic characters not recorded in *Allosaurus,* including the high, short skull, frontal horns, a weak contact between the dentary-splenial and postdentary bones, hypertrophy of epipophyses and atrophy of the neural spines of the cervicals (Fig. 34), strong fusion and size reduction of the sacral centra, unique uncinate processes of the anterior caudals, and the extreme reduction of the forearm bones (Fig. 34G, I).

We consider these differences sufficient to demonstrate that the Allosauridae and Abelisauridae are separate taxonomic entities, widely separated by their morphology. They diverged from an evolutionary stage prior to *Allosaurus,* perhaps not far from *Piatnitzkysaurus* of the Middle Jurassic.

### Comparison with Ceratosauridae

The Ceratosauridae is a monotypic family of the Late Jurassic that, because of its peculiar anatomy, stimulated the interest of several workers (Marsh, 1884; 1896; Gilmore, 1920; Huene, 1926). *Ceratosaurus nasicornis* Marsh, from the Morrison

Formation, Fremont County, Colorado, has several distinctive characters upon which the family Ceratosauridae Marsh was based. According to Gilmore (1920), the poor definition of the family was the main reason for the rejection of the new family by paleontologists of the time. However, Gilmore (1920) restudied *Ceratosaurus* and reaffirmed the validity of the family.

If, as indicated by Gilmore (1920), *Ceratosaurus* has several plesiomorphic characters that identify it as one of the more primitive post-Trassic Theropoda, it is also true that it bears several derived characters that show specialized features of its anatomy. We do not believe the derived characters of the sacrum and ilia were ever evaluated in *Ceratosaurus,* and we think that these characters reveal specialized features not recorded in contemporaneous Carnosauria. The number of vertebrae forming the synsacrum, the degree of ossification, and the secondary reduction in size of the five fused centra represent a suite of derived characters not recorded in other Jurassic or Cretaceous Carnosauria of the Northern Hemisphere. The synsacrum of *Ceratosaurus* includes two anterior vertebrae that serve a sacral function ("presacrals 22 and 23") and a posterior sacral, indicated as "caudal 1" (Gilmore, 1920: pl. 21). Such a specialized sacrum fits between the extended ilia of *Ceratosaurus,* which are relatively more developed and derived than in *Allosaurus.* The ratio between the lengths of the radius and femur of *Ceratosaurus* and *Allosaurus* also illustrates the degree of limb disparity; the ratio is more derived in *Ceratosaurus* than in *Allosaurus.* The radius of *Ceratosaurus* is 24% the length of the femur, whereas in *Allosaurus* (USNM 4734) it is 28%. This may be a good indication, when considered with the other characters cited above, that *Ceratosaurus* was not the most primitive of the post-Triassic theropods, but an adaptive type characterized by a mix of plesiomorphic and apomorphic characters that followed a different evolutionary path than did the Allosauridae-Tyrannosauridae line.

In spite of the different ages of *Ceratosaurus* (Late Jurassic) and of *Carnotaurus* (Middle or Late Cretaceous) and the presence in both genera of very different characters, we believe that they share a common ancestor. Both represent a comparable adaptive level based on the plesiomorphic and apomorphic characters they share.

We shall consider first the similarities and then the differences. In addition to the skulls being similar in the height of the premaxilla in the narial region, they have: a small maxillary fenestra located near the preorbital opening; a jugal that lacks an anterior projection overlying the maxilla and which does not border the preorbital opening; a large infratemporal opening, without an anterior projection of the quadratojugal and squamosal; a dorsoventrally long quadrate; and a squamosal with a slender, rod-like ventral projection, not oriented anteroventrally.

There are many similarities in the postcranial skeleton: the centra are well fused in the sacrum and secondarily reduced; the pelvis (Fig. 35A, B) is axially elongated; the pubis has the obturator foramen surrounded by bone; there is a large laminar contact between pubis and ischium; the ischium has a distal expansion; the femoral head is lower than the major trochanter and directed anteromediad; the lesser trochanter is poorly developed dorsally; and digits of the manus have short phalanges. The more significant differences between the genera include three premaxillary teeth in *Ceratosaurus* and four in *Carnotaurus;* an absence of nasal horn or lachrymal protuberances in *Carnotaurus;* an absence of frontal horns in *Ceratosaurus;* skull short and high in *Carnotaurus;* lachrymal posteriorly convex in *Carnotaurus;* anterior projection of postorbital absent in *Ceratosaurus;* a very wide jugal in *Carnotaurus;* more developed mandibular fenestrae in *Carnotaurus;* cervical vertebrae that are basically different, being much more derived in *Carnotaurus* (Fig. 34D, B); anterior caudal vertebrae more derived in *Carnotaurus;* and major differences in the humerus (Galton and Jensen, 1979: fig. 3T) and in the forearm bones.

Some of these differences rule out the possibility that *Ceratosaurus* was in an ancestral position to *Carnotaurus.* These include the nasal and lachrymal protuberances and the presence of only three teeth in the premaxilla. Other important characters, such as the peculiar morphology of the cervical and caudal vertebrae of *Carnotaurus,* do not have any morphological similarities in *Ceratosaurus,* preventing us from relating these two genera directly.

Finally, the similarities, even ignoring those that are plesiomorphic characters, are broad enough to suggest a significant, close phylogenetic relationship between *Ceratosaurus* and *Carnotaurus.* At present it is not easy to define such a relationship, but it is obviously closer than with any other family of Carnosauria. This means that in spite of several good differences at the family level, Ceratosauridae and Abelisauridae appear to be related, and they may belong in the same superfamily. Such an arrangement may be useful to unite them and, at the same time, distinguish them from the remaining families of Carnosauria.

## Comparison with Theropods from Egypt and India

The theropod remains from the Cenomanian of Baharija, Egypt, include significant remains of Carnosauria. They correspond to *Spinosaurus aegyptiacus* Stromer, 1915, *Carcharodontosaurus saharicus* Stromer, 1931, and *Bahariasaurus ingens* Stromer, 1934. According to Stromer, these three genera are characterized by elongate, slender appendicular bones, without large expansions in the distal end of the femur. In the case of *Bahariasaurus,* there are plesiomorphic characters in the proximal region of the femur, with the femoral

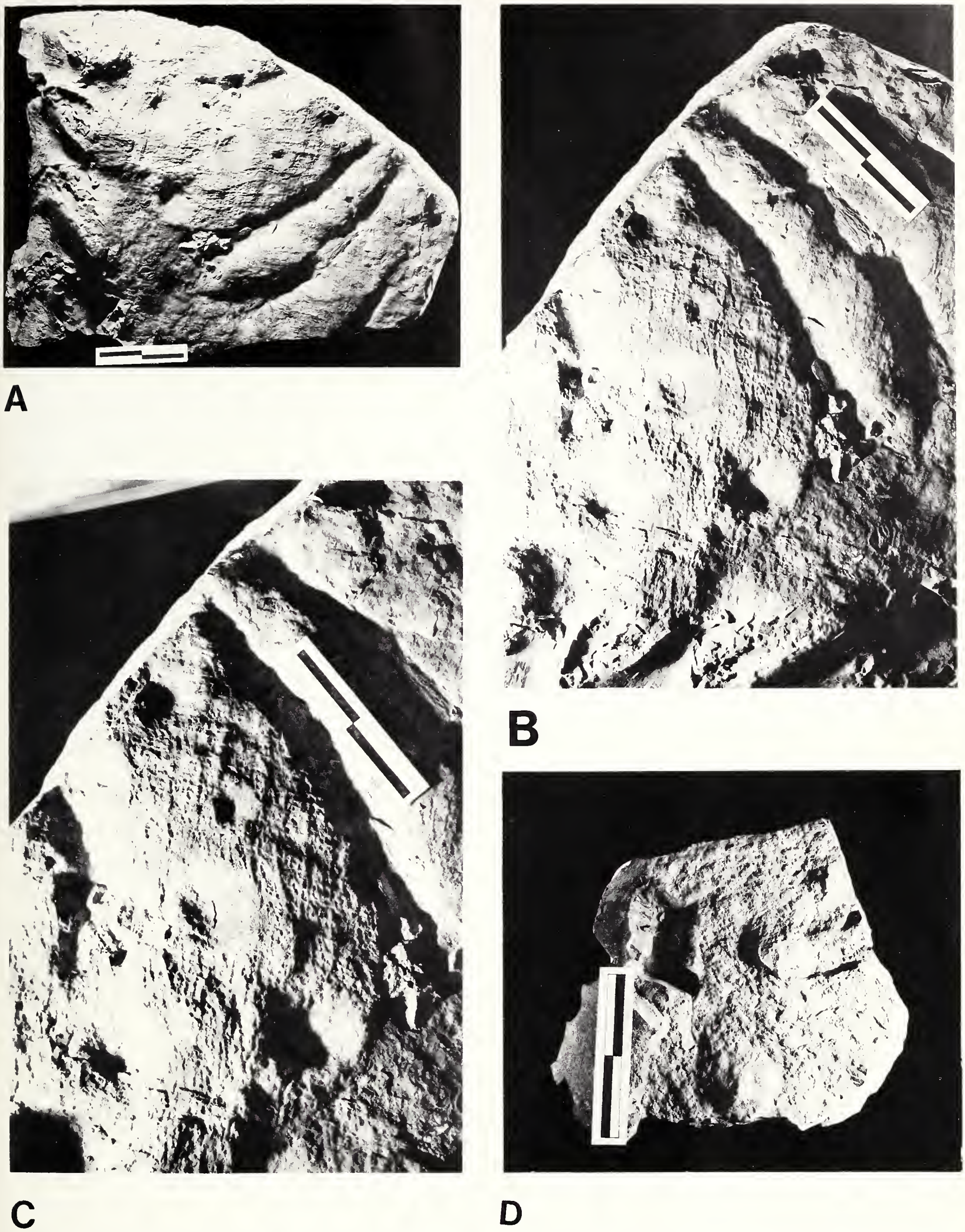

**Figure 37.** *Carnotaurus sastrei.* Skin impressions corresponding to the proximal caudal region (**A**) and details of the same (**B, C**). The parallel depressions correspond to the haemal arches. Scale = 10 cm.

head projecting medioanteriad and lower than the major trochanter.

The possibility of comparison between the African forms and the Abelisauridae (*Abelisaurus, Carnotaurus,* and *Xenotarsosaurus*) are limited because of the fragmentary condition of the former, by the notable derived characters of the *Spinosaurus* vertebrae, and in part, too, because the African

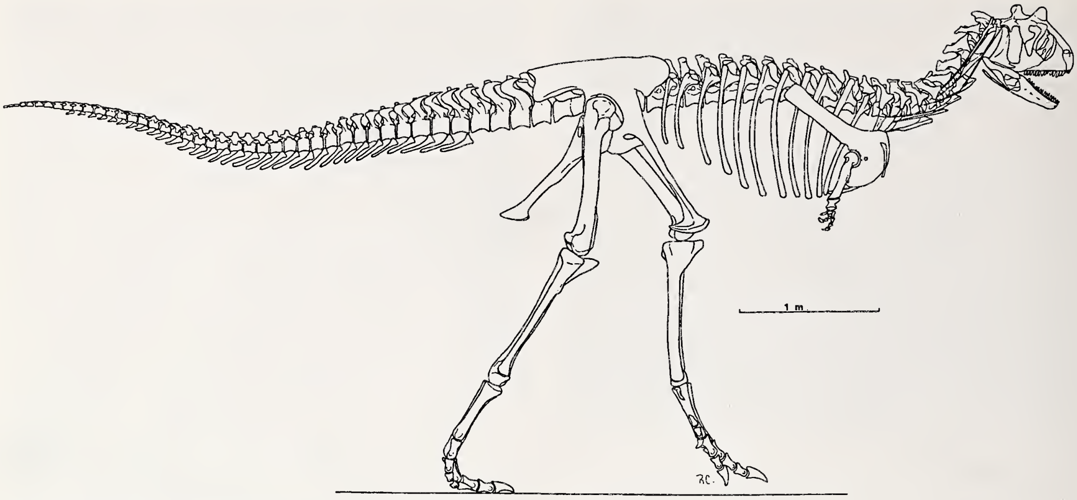

**Figure 38.** *Carnotaurus sastrei.* Reconstruction of the skeleton.

specimens were damaged or destroyed during World War II. But, in spite of the limitations, there are anatomical features that suggest more similarities between *Carnotaurus* (Abelisauridae) and the African forms than between Abelisauridae and Tyrannosauridae. For example, there are indications that the basic characters of the hindlimb of *Carnotaurus* and the African forms are very similar and differ markedly from those of the Tyrannosauridae. Characters of the latter include a robust femora, with the proximal head projecting mediad and higher than the major trochanter and with the lesser trochanter more dorsally developed.

We do not have sufficient information to evaluate the validity of the Spinosauridae; however, the vertebral characters and the features of the lower jaw and teeth appear to be sufficiently derived to recognize it as valid.

From a paleobiogeographic approach, it has been considered that the Spinosauridae and Abelisauridae would be endemic families for the Cretaceous of Gondwana (Bonaparte, 1986b), whereas the Tyrannosauridae appear to be endemic to Laurasia. If this interpretation, based on paleogeographic events of great magnitude, such as the separation of Laurasia and Gondwana before the end of the Jurassic, is correct, we can hypothesize that the few similarities cited between the African and South American Middle and Late Cretaceous Carnosauria result from a common biogeographic history.

The carnosaurs from the Upper Cretaceous of India, *Indosaurus mattleyi* (Huene and Mattley, 1933), and *Indosuchus raptorius* (Huene and Mattley, 1933), were reviewed by Walker (1964) and by Chatterjee (1978). The latter described new material of *Indosuchus* stored at the AMNH. Chatterjee agreed with Walker's interpretation that *Indosaurus* is a megalosaurid (=Allosauridae) and that *Indosuchus* is a tyrannosaurid. The assignment of *Indosuchus* to the Tyrannosauridae appears without basis, primarily because the maxilla of *Indosuchus* lacks the typical maxillary fenestra of the tyrannosaurids.

Our interpretation of *Indosuchus* is that it represents a different family than the Tyrannosauridae, possibly corresponding to the Abelisauridae, in which the maxillary fenestra exists in a reduced form within the main preorbital vacuity.

We do not have enough information for a full systematic evaluation of *Indosaurus;* however, we call attention to the imprecise suggestion that it is a "megalosaur" (Chatterjee, 1978: 573), which means less than to say "carnosaur." This assignment was based on fragments discovered in latitudes very distant from where Jurassic megalosaurs are recorded. Lacking the necessary evidence, we believe it is better to suggest that *Indosaurus* may represent a new, unknown family rather than force geography and chronology by identifying it with European or North American forms.

### Summary

Comparisons of *Carnotaurus sastrei* with other species of Carnosauria allow the following interpretations:

1. The cranial characters of *Carnotaurus sastrei* are good indicators of familial affinities with *Abelisaurus comahuensis,* type species of the family Abelisauridae Bonaparte and Novas, 1985. This permits reference, without doubt, of *C. sastrei* to that family of Carnosauria.
2. As indicated in the description and in comparisons with Cretaceous theropods of Laurasia, the Abelisauridae have a suite of characters that distinguish them from the several theropod families of that supercontinent, especially the Tyrannosauridae.
3. The phylogenetic relationship between the

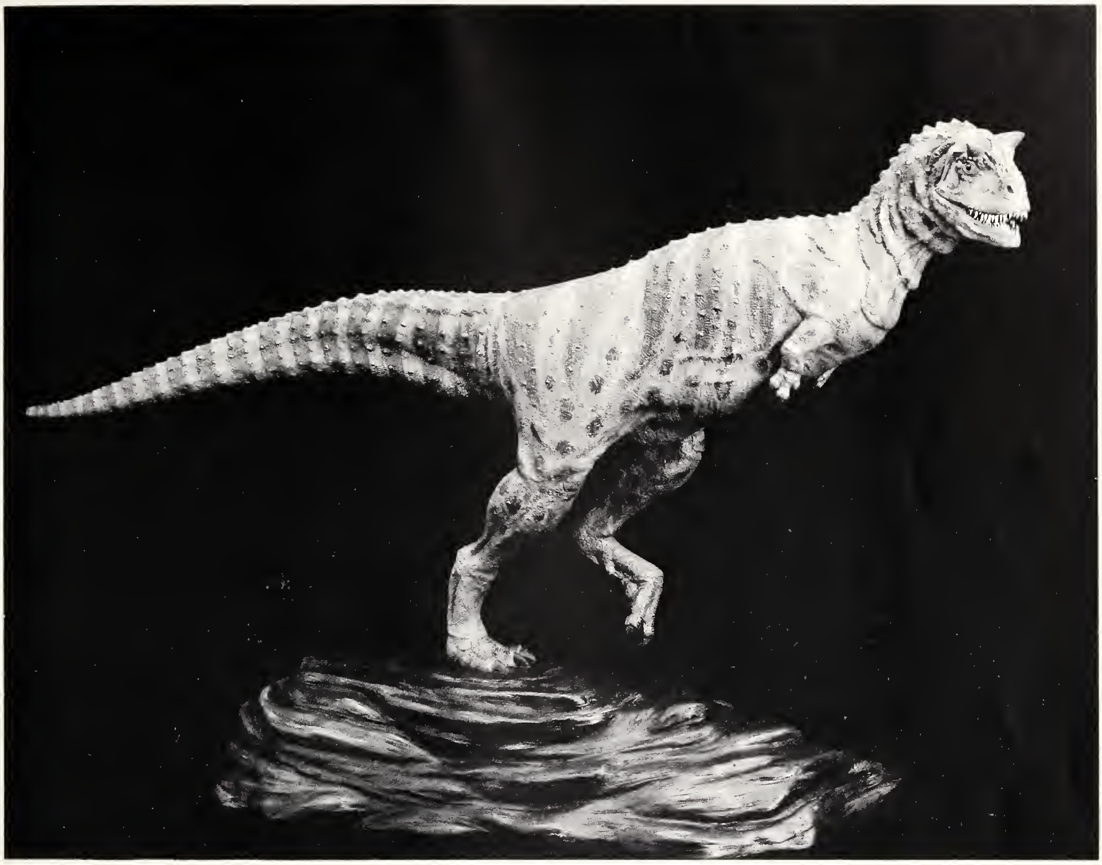

**Figure 39.** *Carnotaurus sastrei.* Model by Stephen Czerkas.

Abelisauridae and Noasauridae, based on the morphology of the maxilla, quadrate, squamosal, and cervical neural arch, appear convincing in view of the following synapomorphies: significant reduction of the additional preorbital opening, reduction of the cervical neural spines, strong anteriad development of the epipophyses, and the lateral crest from the epipophyses. We interpret these characters as suggesting a monophyletic relationship for the two families.

4. Theropods from the Cenomanian of Egypt resemble the Abelisauridae more than the Tyrannosauridae, at least in the hindlimb organization.

5. Comparisons between *C. sastrei* and Jurassic theropods suggest that the Abelisauridae, and probably Noasauridae, may by phylogenetically related to the Ceratosauridae, but we cannot clearly define this relationship at present. The phylogenetic relationship may be one of common ancestry at the familial level, based on the common possession of several apomorphic characters, such as sacrum with several fused vertebrae with reduced centrae, anteroposteriorly elongated ilium with extended supra-acetabular crest, the ischia distally expanded as a "foot," and a very slender pubis shaft. Several plesiomorphic characters, *e.g.*, a large infratemporal opening, manus with four digits, obturator foramen enclosed by bone, poor development of the lesser trochanter, femoral head medioanteriorly projected, have also been noted.

## DISCUSSION

The comparisons of *Carnotaurus sastrei* with other theropods have permitted us to recognize similarities and differences at different levels, with taxa from South America and other continents.

The phylogenetic relationship between the Allosauridae and Tyrannosauridae that is recognized by some authors (Paul, 1984; Gauthier, 1986) appears well based, and it seems to represent one of the main lineages of the Carnosauria. Another lineage, of similar importance, is formed by the Ceratosauridae-Abelisauridae-Noasauridae. We hypothesize that from Jurassic ancestors of Pangean distribution two vicariant groups developed, leading to the Cretaceous families Tyrannosauridae in Laurasia and Abelisauridae in Gondwana.

Following the results of the comparisons detailed above, we believe it is convenient to recognize a systematic entity at the superfamily level—the Ceratosauroidea—to contain the Ceratosauridae, Abelisauridae, and Noasauridae, whose main radiation and Cretaceous evolution was in Gondwana.

The systematic interpretation of this hypothesis may be stated as:

Superfamily Tyrannosauroidea
Family Allosauridae
Family Tyrannosauridae

Superfamily Ceratosauroidea
Family Ceratosauridae
Family Abelisauridae
Family Noasauridae

This interpretation presents us with the novel opportunity of interpreting as carnosaurs a family—the Noasauridae—to date known only from small-sized species such as *Noasaurus leali*, which has a skull approximately 10 to 12 cm long. The interpretation is based on the synapomorphies of the maxilla and peculiar characters of the cervical neural arch. The presence of Noasauridae among the Carnosauria, an infraorder normally characterized by large predators, may relate to the long isolation of the Gondwana continents through the Cretaceous (Bonaparte, 1986b) and the apparent absence of Coelurosauria in the Cretaceous of Gondwana. The Cretaceous isolation of both supercontinents would have provided an opportunity for the Gondwanian Carnosauria to occupy the ecological niches of small predators.

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# *CHOROCARIS VANDOVERAE,* A NEW GENUS AND SPECIES OF HYDROTHERMAL VENT SHRIMP (CRUSTACEA, DECAPODA, BRESILIIDAE) FROM THE WESTERN PACIFIC

JOEL W. MARTIN[1] AND ROBERT R. HESSLER[2]

**ABSTRACT.** A new genus and species of bresiliid shrimp, *Chorocaris vandoverae,* is described from hydrothermal vents in the Mariana Back-Arc Basin, a spreading center in the western Pacific. The genus is morphologically close to *Rimicaris,* a genus known from vents along the north Mid-Atlantic Ridge. Characters that distinguish *Chorocaris* from *Rimicaris* include a third maxilliped composed of three (rather than four) long segments, a more concave pterygostomial border of the carapace, and a wide, blunt rostrum. The two genera differ also in the morphology of the orbital region, antennae, and third maxilliped. In *Rimicaris,* the antennal area is slightly opercular, meeting the branchiostegal border and covering the mouthparts, whereas this region is normal in *Chorocaris. Rimicaris chacei* is transferred to *Chorocaris,* leaving *Rimicaris exoculata* the sole species in *Rimicaris.* The discovery of *Chorocaris* in the western Pacific, in conjunction with other recent finds of Pacific and Atlantic vent species, indicates a possible faunal connection between western Pacific and Mid-Atlantic vent areas. A key to the currently accepted genera of the Bresiliidae is included.

## INTRODUCTION

Two genera of caridean shrimp have been previously reported from the vicinity of marine hydrothermal vents. The genus *Alvinocaris* was erected by Williams and Chace (1982) to accommodate *A. lusca,* an unusual bresiliid shrimp from thermal vents of the Galapagos Rift. Characters of *Alvinocaris* were such that the family Bresiliidae, already recognized by most workers as an unnatural assemblage, had to be slightly redefined and expanded to accommodate the new genus (Williams and Chace, 1982). Three additional species of *Alvinocaris* were later reported from the Atlantic and Gulf of Mexico (Williams, 1988). The genus *Rimicaris* was erected by Williams and Rona (1986) to accommodate two new species of the Bresiliidae from hydrothermal vents along the Mid-Atlantic Ridge at 26°N. Additional Mid-Atlantic Ridge records (23°22′N) for the two species of *Rimicaris* were reported by Williams (1987), and the genus received popular attention when it was discovered that one of the two species, *R. exoculata* Williams and Rona, 1986, has, in lieu of normal eyes, a pair of large organs just below the cuticle of the cephalothorax. These organs contain rhodopsin and apparently function in light perception (Van Dover *et al.,* 1989; Pelli and Chamberlain, 1989).

A. B. Williams (personal communication) was aware at the time of the original description of *Rimicaris* that the two species (*R. exoculata* and *R. chacei*) differed in many respects, but because the available material was rather limited, and because the two species shared many characters, he refrained from erecting a second genus for *R. chacei.* The present paper is based on a relatively large collection of shrimp from hydrothermal vents along the Mariana Back-Arc Spreading Center in the western Pacific. This new material has allowed us to describe a new genus and species of the Bresiliidae and to reconsider the generic placement of *R. chacei* Williams and Rona, 1986, which is herein transferred to our new genus, *Chorocaris.* The number of known bresiliids is raised to nine genera and 17 species.

## METHODS AND MATERIALS

Shrimp were collected during a series of dives with the submarine *Alvin* in April and May, 1987. The collection sites consisted of three active vent fields along the spreading center of the Mariana Back-Arc Basin at about 18°N, just west of the Mariana Island Arc, at depths of 3595–3660 m (Hessler *et al.,* 1988; Hessler and Martin, 1989). The shrimp, which lived in profusion at vent openings or in the immediately adjacent rocks, were collected with

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[1] Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

[2] Scripps Institution of Oceanography, La Jolla, California 92093.

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nets manipulated by the mechanical arm of the submarine. Most of the shrimp were fixed in 4% buffered formalin and stored in 80% ethanol. Others were frozen for physiological analyses. Drawings were made with a Wild M5APO dissecting stereoscope with camera lucida. Morphological comparisons were facilitated by the following clearing and staining protocol. Specimens were macerated in warm potassium hydroxide, rinsed with water, and stained with aqueous aniline blue before stepwise dehydration in ethanol. Alcoholic specimens (in absolute ethanol) were then transferred to Terpineol®, a commercially available mixture of oils that is slightly miscible with water, maintains flexibility of specimens, and greatly enhances visibility of cuticular structures.

## SYSTEMATICS

## *Chorocaris* new genus

*Rimicaris* Williams and Rona, 1986:447 (in part; *R. chacei* only).

**DIAGNOSIS.** Carapace smooth, spineless, pterygostomial margin slightly concave. Rostrum wide and blunt, unarmed, nearly reaching or exceeding postorbital prominences in length. Eyestalks cylindrical, fused medially, lacking pigment in adults. Antenna 2 scale broadly oval, with distinct notch on distolateral border. Mandible with 2-segmented palp, distinct separation between incisor and molar processes. Second maxilla with scaphognathite greatly expanded anteriorly and conspicuously setose. First maxilliped with greatly expanded exopod, similar to scaphognathite. Second maxilliped with merus and ischium short, stout, as wide or wider than dactylus. Third maxilliped composed of 3 long segments and 2 shorter basal segments. Telson with 6–9 pairs of submarginal dorsal spines and usually 2 pairs of posterolateral spines. Branchial formula as in *Rimicaris* and *Alvinocaris* (see Williams, 1988). Male anatomy not known.

**TYPE-SPECIES.** *Chorocaris vandoverae,* new species.

**ADDITIONAL SPECIES.** *Rimicaris chacei* Williams and Rona, 1986.

**ETYMOLOGY.** From the Greek words *choros* (dance) and *karis* (shrimp), in reference to the rapid, active, demersal behavior of these shrimp. The gender is feminine.

## *Chorocaris vandoverae* new species

Figures 1, 2, 3a–e

**MATERIAL.** 119 adults, all apparently females, from the following dives:

Dive 1835, 26 April 1987, Snail Pits portion of Burke vent field, 3660 m, 18°10.948′N, 144°43.204′E, 37 shrimp (4 missing).

Dive 1836, 27 April 1987, Burke vent field (both Snail Pits and Anemone Heaven portions), 3660 m, 18°10.917–18°10.948′N, 144°43.210–144°43.204′E, 42 shrimp (35 frozen).

Dive 1837, 28 April 1987, Burke Field, 3660 m, 18°10.0′N, 144°43.2′E, 10 shrimp (all frozen).

Dive 1843, 4 May 1987, Alice Springs vent field, 3640 m, 18°12.599′N, 144°42.431′E, 30 shrimp (1 of which was dissected and used for illustrations herein).

**TYPE MATERIAL.** Holotype female, Dive 1843, National Museum of Natural History, Smithsonian Institution, USNM 243946. Designated paratypes have been deposited in the National Museum of Natural History (10 females, Dive 1843, USNM 243947); the Natural History Museum of Los Angeles County, Los Angeles, California (12 females, Dive 1835, LACM 87-272.1; 7 females, Dive 1836, LACM 87-273.1; 7 females [1 dissected], Dive 1843, LACM 87-274.1); and the Muséum National d'Histoire Naturelle, Paris, France (10 females, Dive 1843, MNHN-NA 11924). All additional material (i.e., not designated paratypic) listed above is in the Scripps Institution of Oceanography, La Jolla, California.

Several specimens that were not examined in preparing the description, but that are almost certainly this species because they were taken from the same collections, are in the personal collections of R.R. Hessler, C.L. Van Dover, S. Ohta, and the Emperor of Japan.

**MEASUREMENTS.** Carapace length (CL) from 5.7 to 15 mm, total length (TL) from 16.3 to 52 mm (N = 34); holotype CL 15 mm, TL 52 mm.

**DIAGNOSIS.** Rostrum clearly exceeding anterior-most projection of postorbital prominence. First pereiopod with distomedial carpal cleaning brush.

### DESCRIPTION

**CARAPACE (Figs. 1a–d).** Smooth, with minute scattered setae. Not laterally inflated (compare to *Rimicaris*). Frontal dorsal border produced into blunt rostrum that exceeds acute postorbital prominences (Fig. 1d, arrow). Anterolateral (pterygostomial) border slightly concave between ventrolateral projection and postorbital prominence. Ventrolateral projection extending anteriorly beyond level of rostrum. Slight groove extending posterolaterally

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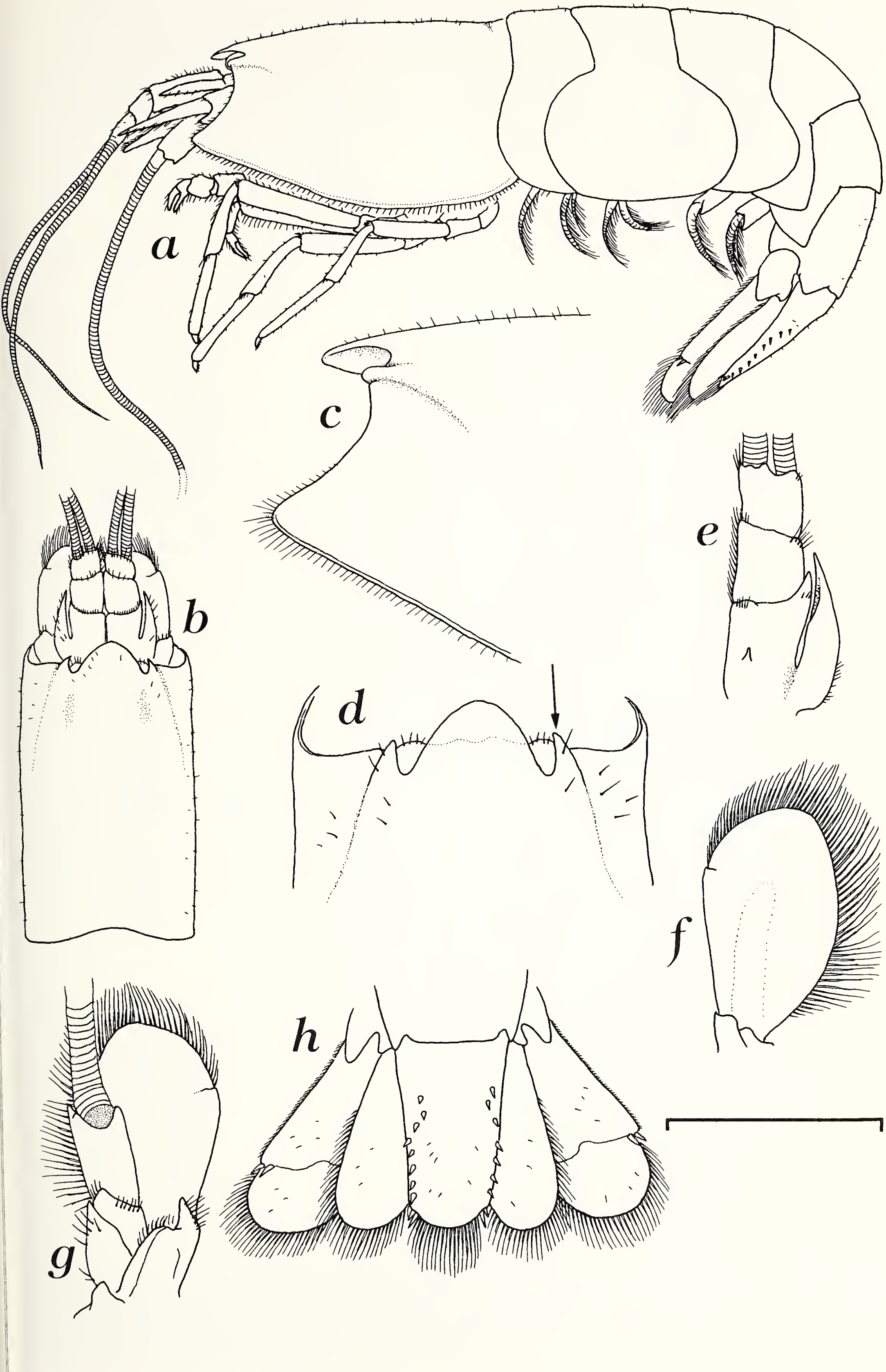
**Figure 1.** *Chorocaris vandoverae,* female paratype from LACM 87-274.1: carapace, antennae, abdomen, and uropods. a, Entire animal, lateral view; **b**, dorsal view of carapace and bases of antennae; **c**, frontal region of carapace, lateral view, eyestalks removed; **d**, dorsal view of frontal region of carapace and eyes, arrow indicating acute postorbital prominence; e, left first antenna peduncle, ventral view; **f**, left antennal scale, dorsal view; **g**, left antennal scale and antennal peduncle, ventral view; **h**, telson and uropods. All figures except b from the same individual. Scale bar = 10.0 mm for a, b; 5.0 mm for c–g; 6.5 mm for h.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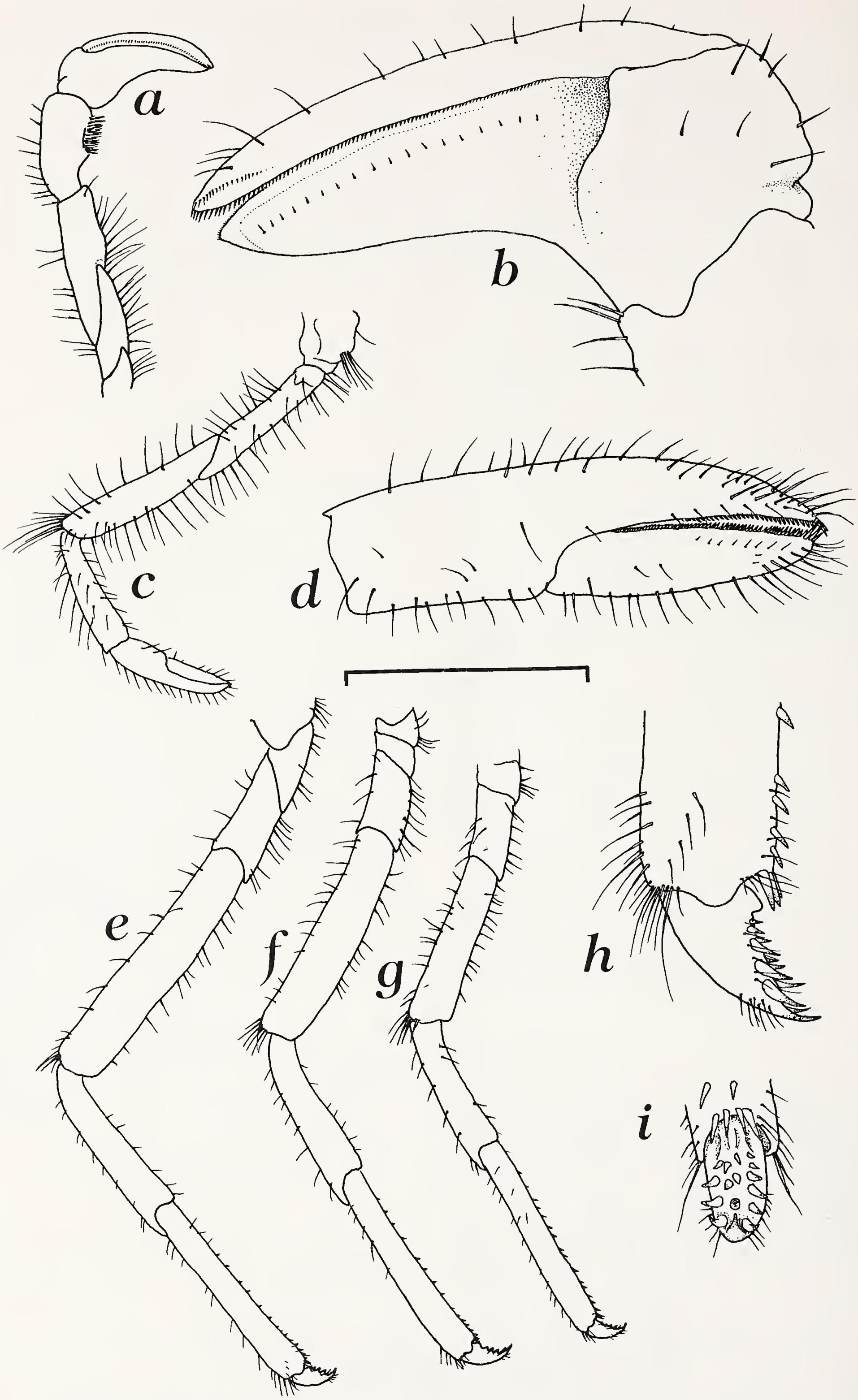

Figure 2. *Chorocaris vandoverae,* female paratype from LACM 87-274.1: pereiopods. **a,** Cheliped, dorsomedial view; **b,** "inner" view of chela; **c,** second pereiopod; **d,** chela of second pereiopod; e–**g,** third through fifth pereiopods; **h, i,** lateral and posterior views (respectively) of dactylus of third pereiopod. Scale bar = 5.0 mm for a, c, and e–g; 1.25 mm for all others.

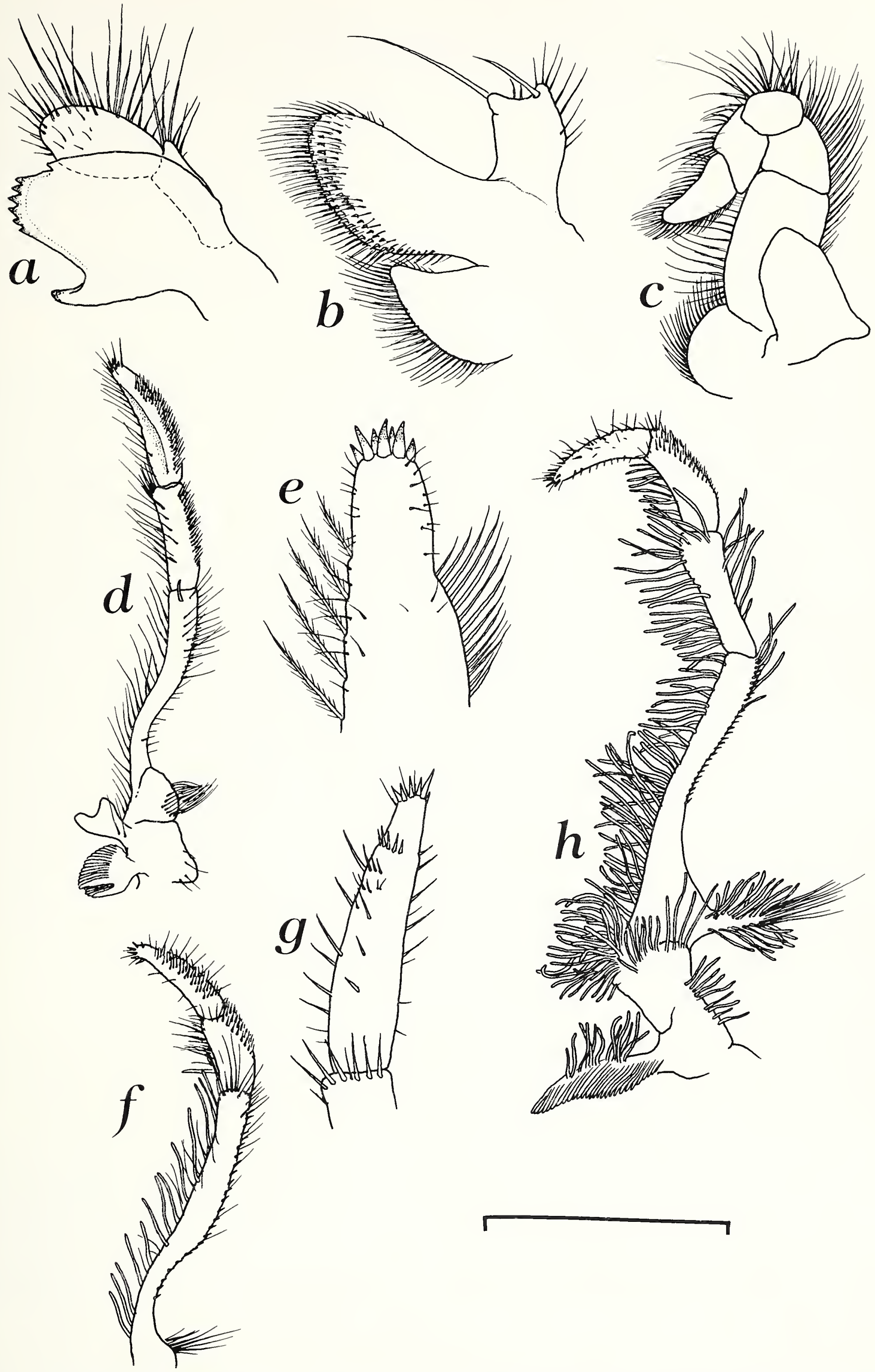

**Figure 3.** *Chorocaris vandoverae,* female paratype from LACM 87-274.1 (a–e); *Chorocaris chacei,* female paratype LACM 85-174.1 (f, g); and *Rimicaris exoculata,* female paratype LACM 85-174.2 (h): selected mouthparts. *Chorocaris vandoverae*: **a,** left mandible, "outer" view; **b,** first maxilla; **c,** second maxilliped; **d,** third maxilliped, right side, ventral view; **e,** tip of terminal segment of third maxilliped. *Chorocaris chacei*: **f,** third maxilliped, ventral view, penultimate segment appearing shorter because of bend toward viewer; **g,** distal segment of third maxilliped. *Rimicaris exoculata*: **h,** third maxilliped, ventral view. Scale bar = 5.0 mm for d and h, 1.25 mm for a, b, e, and g; 2.5 mm for c and f.

from lateral border of each postorbital prominence. Dorsal surface immediately posterior to lateral extent of each eyestalk with ill-defined pigmented areas running longitudinally; carapace otherwise uniformly off-white.

**EYES (Figs. 1a, d).** Reduced, just visible in dorsal view between rostrum and postorbital prominences, with few setae on anterior surface of nonfaceted cornea. Pigment lacking, except slight pigmentation in lateral extremity of eyestalk in some juveniles. Eyestalks cylindrical, fused and contiguous medially (Fig. 1d).

**ANTENNAE.** Antenna 1 peduncle (Fig. 1e) with obvious tooth on ventral surface of basal segment and sharp anteriorly directed spine or tooth distolaterally. Stylocerite acute, extending almost to distal border of second peduncular segment, slightly concave mesially. Antenna 2 (Figs. 1b, f, g) with oval scale bearing slight notch at distal third of mesial border; dorsally with slight central longitudinal ridge; ventrally as shown (Fig. 1g).

**PEREIOPODS.** Cheliped (Figs. 2a, b) stout, slightly twisted, with distinct carpal brush and with chela strongly curved inward; proximal dorsal border of propodus with groove just distal to articulation with carpus; fingers of chela fringed with small teeth, obvious on dactylus but minute and nearly undetectable on propodus; fixed finger twice length of palm. Second pereiopod (Figs. 2c, d) chelate, dactylus about half length of propodus; fingers armed with even row of small teeth, larger distally. Third through fifth pereiopods (Figs. 2e–i) achelate and similar, with short dactylus bearing basal tooth and several sharp, curved spines on posterior surface.

**MOUTHPARTS.** Mandible (Fig. 3a) with 6–7 similarly sized teeth on incisor process; palp 2 segmented, both segments with long setae. Maxilla 1 (Fig. 3b) with 2 stout setae and several smaller setae on endopod as shown in figure. Maxilla 2 and first maxilliped (not illustrated) hypertrophied and roughly similar to those of *Rimicaris exoculata* and *R.* (now *Chorocaris*) *chacei* (Williams and Rona, 1986). Maxilliped 2 (Fig. 3c) stout, segments wide, dactylus longer than propodus and slightly curved upward distally. Maxilliped 3 (Figs. 3d, e) composed of 3 long segments, the terminal segment possibly representing a fused dactylus and propodus; most proximal of 3 long segments strongly curved.

**BRANCHIAE.** As described for the genus *Rimicaris* by Williams and Rona (1986) and further described for both *Rimicaris* and *Alvinocaris* by Williams (1988).

**ABDOMEN (Figs. 1a, h).** Posterolateral angles of abdominal somites 4–6 becoming sharper posteriorly; somite 2 with greatly expanded pleura as wide or wider than height of carapace, posterolateral margin rounded; somite 3 with posterolateral angle rounded. Telson (Fig. 1h) with 7–9 pairs of spines on dorsal border, number occasionally differing from side to side; posterior border with 2 pairs of posterolateral spines, inner pair longer; outer branch of uropod with 2 stout spines on external (lateral) border of diaresis.

**PLEOPODS (not illustrated).** Similar to those illustrated by Williams and Rona (1986) for *Rimicaris chacei.*

**ETYMOLOGY.** We are pleased to name this species for Cindy Lee Van Dover in recognition of her stimulating contributions to the biology of hydrothermal vent decapods.

## COMPARATIVE MORPHOLOGY OF *RIMICARIS* AND *CHOROCARIS*

### ORBITAL REGION

*Rimicaris exoculata* was originally described as lacking any eyes (Williams and Rona, 1986). Although it is true that the typical cylindrical eyestalk seen in other caridean shrimp is lacking, we believe that the eyestalk is present but is greatly reduced and modified. This is best illustrated by comparing the derived genus *Rimicaris* with the relatively primitive *Chorocaris.* In *Chorocaris* the eyestalks are medially fused, so that in dorsal or frontal views the fused stalks appear as a single transverse cylinder. In dorsal view the medial portion of this cylinder is concealed by the rostrum, although in cleared specimens (see Methods and Materials) the entire cylinder is apparent in dorsal view (Fig. 1d). If the rostrum is missing, or markedly reduced as in *Rimicaris,* then the fused eyestalks are readily visible. The flattened transverse plate in the orbital area of *Rimicaris exoculata* is, we believe, just a further modification of the transverse, nonfunctional, fused eyestalk seen in *Chorocaris.* This condition was suspected by Williams and Rona (1986) and is indicated in their terming this greatly modified eyestalk the transverse ocular plate. We have labeled this flattened eyestalk op (for ocular plate) in Figures 4a and 4b.

### FRONTAL REGION

The frontal region of *Rimicaris exoculata* is unique among all known caridean shrimp. The stylocerite of the first antenna and the scaphocerite of the second antenna are both very broad and flat. This in itself is not unusual, but these plates also fit tightly against one another and against the other antennal components of the frontal region, all of which are also flattened, with the result being an opercular plate-like shielding of the mouthparts. The opercular effect is facilitated by a lateral, basal projection of the first antenna peduncle that slightly exceeds the lateral extension of the base of the scaphocerite. This rather blunt projection, visible in the ventral view of the antennal peduncle given by Williams and Rona (1986:452, fig. 6a), creates a slot between itself and the ventral surface of the scaphocerite blade. The slot accommodates the upper pterygostomial border of the carapace, and the resulting fit of the carapace border into this slot enhances the opercular nature of the frontal region

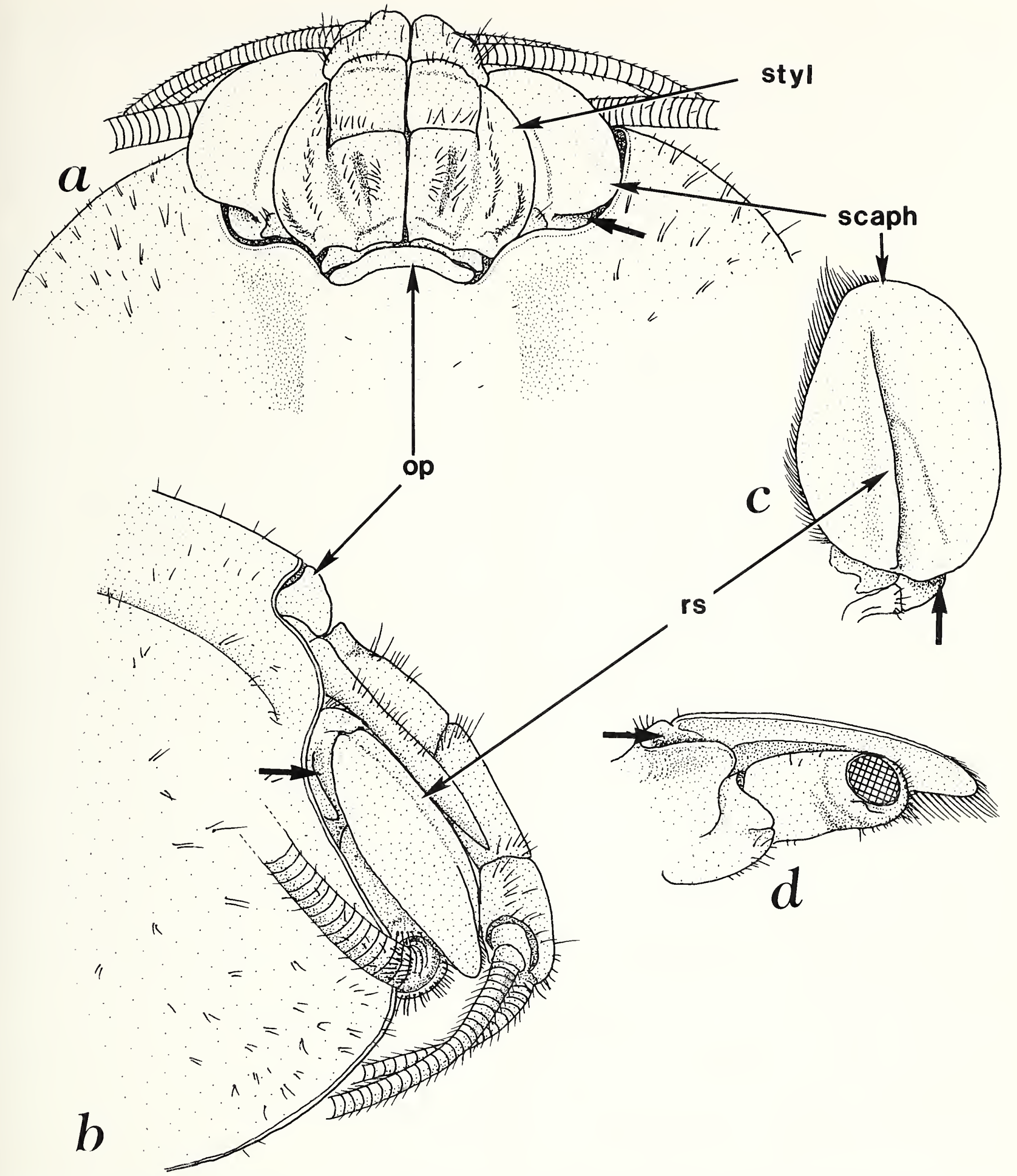

**Figure 4.** Frontal region of *Rimicaris exoculata,* female paratype from LACM 85-174.2. **a,** Dorsal view of anterior carapace and bases of antennae 1 and 2; **b,** lateral view of anterior carapace and bases of antennae 1 and 2; **c,** dorsal view of scaphocerite of antenna 2; **d,** lateral view of scaphocerite illustrated in c, hatching represents removed flagellum of antenna 2. Abbreviations: styl = stylocerite of antenna 1; scaph = scaphocerite of antenna 2 (antennal scale); op = opercular plate (fused and flattened eyestalks); rs = dorsal ridge of scaphocerite. Heavy arrows indicate slot between antenna 2 scale and peduncle that accommodates anterior border of carapace, making a seal between operculum and pterygostomial margin of carapace; see text.

of the shrimp (Figs. 4a–d, heavy arrow). The expanded frontal region of the shrimp thus shields the mouthparts dorsally. The greatly inflated carapace is distended to the point that the anteroventral borders nearly touch each other ventrally, thus shielding the mouthparts to a lesser degree ventrally as well. Williams and Rona (1986:452) noted that all legs and even the antennal flagellum "are capable of being placed under [the] branchiostegite." The dorsal surface of the scaphocerite is also modified, bearing a longitudinal ridge (rs, Figs. 4b, c) that serves to close the gap between the scaphocerite and the segments of the peduncle of the first antenna.

In both species of *Chorocaris*, the frontal region is normal, i.e., there is no tendency for the antennal components to appear or function as an operculum, although a slight longitudinal ridge is present on the scaphocerite (see Fig. 1f). The reason for this modification in *R. exoculata* is unknown.

### MAXILLIPEDS

The third maxilliped of *Rimicaris* is composed of four long segments and one or two fused, shorter, basal segments. In contrast, in both species of *Chorocaris* the third maxilliped is composed of only three long segments and two short basal segments. The most proximal of the long segments in *Chorocaris* probably can be equated with the proximal long segment in *Rimicaris*, as the curvature and general shape is very similar (Figs. 3d-h). It is more difficult to decide which of the more distal segments in *Rimicaris* are the homologues of those in *Chorocaris*. The third maxilliped of *C. chacei* was illustrated as having four segments by Williams and Rona (1986, figs. 9i, j). On closer examination, it appears that the maxilliped is composed of only three long segments, with the distal-most segment slightly constricted at about ¾ its length.

The second maxilliped also differs markedly between *Rimicaris exoculata* and the two species of *Chorocaris*. In *R. exoculata*, this maxilliped is thin, with the merus and ischium elongate and strongly concave along their medial margins (see Williams and Rona, 1986, fig. 6h; Van Dover *et al.*, 1988, figs. 2C, 3). In *Chorocaris* the second maxilliped is much more robust and is at most only slightly concave along the mesial borders of the merus and ischium.

## DISCUSSION

### SYSTEMATICS

Many characters of *Chorocaris* are shared with *Rimicaris*, and this is of course reflected in the original assignment of *C. chacei* and *R. exoculata* to the same genus (*Rimicaris*) by Williams and Rona (1986). Of the characters that we feel are of generic importance, all except one (the reduction in segmentation of the third maxilliped) are probably plesiomorphic; i.e., they are shared by several other bresiliid genera and species. Thus, we feel that *Rimicaris*, with its inflated carapace, opercular frontal region, dorsal "eyespots," and lack of a rostrum, is clearly a derived genus that stemmed from *Chorocaris* or some other morphologically similar deep-sea shrimp. The establishment of *Chorocaris* necessitates modifying the diagnosis of *Rimicaris*, as it originally included a species (*R. chacei*) that we transfer to *Chorocaris*. Additionally, we think it is possible that the eyestalks in *Rimicaris exoculata* are reduced, flattened, and nonpigmented, rather than absent (Figs. 4a, b). The modifications to the Williams and Rona (1986) diagnosis of *Rimicaris*, which now is monotypic, are as follows.

### ***Rimicaris*, Emended Diagnosis**

Carapace greatly inflated laterally. Pterygostomial margin convex. Rostrum absent; median frontal region of carapace greatly recessed. Eyes lacking pigment, eyestalks flattened, completely fused medially, visible in dorsal view. Antennal scale broadly oval with margin smooth, lacking dorsal distolateral notch or groove. Antennal scale, bases of antennae, and stylocerite closely approximated, forming opercular complex shielding mouthparts; antennal scale bearing dorsal ridge closing gap between scale and stylocerite. Mandible with 2-segmented palp, distinct separation between incisor and molar processes. Second maxilla with scaphognathite greatly expanded anteriorly and conspicuously setose. First maxilliped with greatly expanded exopod, similar to scaphognathite. Third maxilliped with 4 long and 2 short segments. Second maxilliped with merus and ischium extremely narrow, less than width of dactylus, with strongly concave medial border.

There are several other characters that separate *Rimicaris exoculata* from species in *Chorocaris*, but we hesitate to include these as characters of generic importance. These include the following character states in *Rimicaris*: Stylocerite fused to most of lateral margin of podomere (fused only to basal ⅖ of podomere in both species of *Chorocaris*); tip of stylocerite reaching or just exceeding distal end of podomere 2 (short of that in *Chorocaris*); podomeres of antenna relatively slender (stout in *Chorocaris*); cheliped lacking carpal cleaning brush (see Bauer, 1981) (cheliped with carpal brush in *C. vandoverae* and to a lesser extent in *C. chacei*).

The more slender second maxilliped of *Rimicaris* as compared with *Chorocaris*, a difference noted in the above modifications to the diagnosis of *Rimicaris*, is more easily seen in studies of the feeding appendages (see Williams and Rona, 1986, fig. 6h; Van Dover *et al.*, 1988, fig. 2C).

The two species of *Chorocaris* are rather easy to distinguish. The rostrum is more pronounced in *C. vandoverae*, clearly exceeding the postorbital prominences, whereas in *C. chacei* the rostrum reaches or barely exceeds these prominences. This difference is even more pronounced in juveniles, where the postorbital prominences are clearly defined in *C. vandoverae* but barely discernable in *C. chacei*. Other differences include a more slender stylocerite and the presence of a larger carpal cleaning brush (Bauer, 1981) in *C. vandoverae*. One difference that might be assumed from the original illustrations of *C. chacei* (as *Rimicaris chacei*) is that the cheliped is more stout, with the finger being only about half the length of the palm. However, in the paratype of *R. chacei* that we examined (one female, Natural History Museum of Los Angeles County, LACM 85-174.1), the cheliped is essentially identical to that seen in *R. exoculata* and C.

*vandoverae,* leading us to believe that the cheliped of the animal figured by Williams and Rona (1986, figs. 10a–c) is perhaps aberrant.

It is interesting to note that no males have been collected for either species of *Chorocaris,* although males were described for *Rimicaris exoculata* by Williams and Rona (1986). Males of *R. exoculata* differ only slightly from females; the endopod of the second pleopod bears a distal notch, and the second pleopod bears an appendix masculina (Williams and Rona, 1986).

With the descriptions of *Alvinocaris, Rimicaris,* and now *Chorocaris,* it is becoming increasingly apparent that the family Bresiliidae is an artificial assemblage. The range of characters exhibited by the nine genera (*Bresilia* Calman, 1896; *Discias* Rathbun, 1902; *Lucaya* Chace, 1939; *Pseudocheles* Chace and Brown, 1978; *Tridiscias* Kensley, 1983; *Alvinocaris* Williams and Chace, 1982; *Rimicaris* Williams and Rona, 1986; *Encantada* Wicksten, 1989; and *Chorocaris*) presently constituting the Bresiliidae (including the former Disciadidae; see Forest, 1977; Forest and Cals, 1977; Chace and Brown, 1978; Williams and Chace, 1982; Williams and Rona, 1986; Williams, 1988) is great, and there is no single character that uniquely defines the group. We think it likely that the group is comprised of several monotypic or low-diversity families. Until such time as a family-wide revision is undertaken, we follow the lead of other workers by expanding once again the limits of the Bresiliidae and incorporating *Chorocaris* into the key to the bresiliid genera below (modified after Williams and Rona, 1986, and Williams and Chace, 1982). The genus *Encantada,* known only from an incomplete description of one badly damaged specimen (Wicksten, 1989), is excluded from the key because so many characters of this genus were not described. Wicksten (1989) places *Encantada* in the *Bresilia* group (which would correspond to couplets 2–4 of the following key), but this placement is tentative in light of the fact that the only known specimen lacks a telson, any pereiopodal exopods, and any of the posterior three pairs of pereiopods.

### KEY TO CURRENTLY ACCEPTED GENERA OF THE FAMILY BRESILIIDAE

1. Eyes absent or lacking corneal facets; telson with 3 or more pairs of dorsolateral spines; first pereiopod with ischium and merus distinct; exopods on first 2 pereiopods at most .... 2

— Eyes faceted and pigmented; telson with 3 or fewer pairs of dorsolateral spines; first pereiopod with ischium and merus fused; exopod present on all 5 pereiopods ............. 5

2. Exopods present on first 2 pairs of pereiopods; second maxilla with endites widely separated, at least 1 strap-shaped; gills reduced, pleurobranchs on somites bearing first 4 pereiopods ................................ *Bresilia*

— Exopods absent on pereiopods; second maxilla with endites broad, not widely separated; gills well developed, arthrobranchs on somites bearing third maxilliped and pereiopods 1–4, pleurobranchs on somites bearing pereiopods 1–5 ........................................ 3

3. Carapace with well-developed, compressed, and pointed rostrum bearing dorsal and ventral teeth; pterygostomial spine present; eyes on separate movable stalks ................ *Alvinocaris*

— Carapace with rostrum absent or at most produced as transverse, convex, and toothless front overhanging fused transverse eyestalks; pterygostomial spine absent; eyestalks reduced, fused medially ........................... 4

4. Carapace inflated; rostrum absent (rostral area recessed); eyestalks flattened; stylocerite, scaphocerite, and peduncle of first antenna fitting tightly together forming anterior opercular region; third maxilliped with 4 long and 2 short segments ...................... *Rimicaris*

— Carapace not inflated; rostrum broad and blunt; eyestalks cylindrical; anterior region not opercular, third maxilliped with 3 long segments and 2 short segments .............. *Chorocaris*

5. Antennal scale narrowing distally, blade not overreaching distolateral spine; mandible without deep division between incisor and molar processes; 3 posterior pereiopods pseudochelate (dactylus opposing terminal propodal spine) ............................ *Pseudocheles*

— Antennal scale broad distally, blade overreaching distolateral spine; mandible with moderate to deep division between incisor and molar processes; 3 posterior pereiopods normal, not chelate ................................ 6

6. Rostrum reaching level of distal end of first antenna peduncle; third abdominal somite forming gibbous cap over base of fourth somite; third maxilliped with terminal segment obliquely truncate distally; first pereiopod with dactylus not semicircular; 3 posterior pereiopods with ischiomeral suture somewhat obscure ...... ................................ *Lucaya*

— Rostrum not reaching level of distal segment of first antenna peduncle; third maxilliped with terminal segment distally lanceolate; first pereiopod with dactylus semicircular; 3 posterior pereiopods with ischiomeral suture distinct 7

7. Supraorbital spine present ........ *Tridiscias*

— Supraorbital spine absent .......... *Discias*

## BIOGEOGRAPHIC IMPLICATIONS

In our earlier paper on Mariana vent crabs (Hessler and Martin, 1989) we refrained from discussing biogeographical implications of the western Pacific vent fauna because so little was known at that time. The discovery of *Chorocaris* adds to a growing body of evidence that there is a faunal connection between the Mariana vent area and the northern Mid-Atlantic Ridge. As unlikely as this may seem, we cite the following evidences in support of the theory. The genus *Chorocaris* is known from these two areas only. A more conservative taxonomic approach, placing our new species in *Rimicaris,* would not eliminate the disjunct distribution, as the genus *Rimicaris* would then be represented in these two areas only. Second, as we mentioned briefly in our paper on vent crabs (Hessler and Martin, 1989), the Mariana vent crab (*Austinograea williamsi*) appears morphologically most similar to *Segonzacia mesatlantica* (Williams, 1988) (formerly *Bythograea*; see Guinot, 1989) from vents along the Mid-Atlantic Ridge. The pattern occurs also in mollusks. The limpet genus *Pseudorimula* McLean, erected for the western Pacific vent species *P. marianae* McLean, 1989, has now been collected from vents along the Mid-Atlantic Ridge (McLean, 1989; James McLean, personal communication, 1989), and a new genus of mussel is known from the Mid-Atlantic and western Pacific only (Grassle, 1989). There are active vents south of the Mariana area. Deep-sea tows in the north Fiji Basin have resulted in photographs of what are undoubtedly bythograeid crabs and galatheid lobsters from vent sites (Honza and Auzende, 1988), and a second species of *Austinograea* Hessler and Martin, 1989, has been collected from deep waters near the Tonga Islands (Daniele Guinot, personal communication, 1989). We propose that the hydrothermal areas of the western Pacific and northern Mid-Atlantic were at one time connected via a series of active vent areas, not necessarily active simultaneously, that extended from the Mid-Atlantic Ridge south to the Atlantic-Indian Ocean Ridge, north along the Southwest Indian Ocean Ridge, Mid-Indian Ocean Ridge, and Southeast Indian Ocean Ridge, and finally north through the various spreading centers of the Indo-West Pacific. There is insufficient evidence for us to hypothesize what direction this faunal interchange might have taken. It should also be noted that at least one species of limpet occurs in both the Mariana and East Pacific/Galapagos vent areas but as yet is not known from the Atlantic (James McLean, personal communication, 1989). Elucidation of the origins and distributions of vent faunas will likely prove a complex problem.

## ACKNOWLEDGMENTS

We thank M. Boudrias, S. France, and S. Ohta for their help in collecting the shrimp; H.G. Kuck, A.B. Williams, and C.L. Van Dover for reviewing the manuscript; and J.H. McLean for sharing with us his knowledge of vent limpets. We especially thank G.C. Steyskal for his help in composing the name of the genus.

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# Contributions in Science

## Discovery of the Family Blephariceridae (Diptera) in Cuba, Including the Description of a New Species

Charles L. Hogue and Gabriel Garcés G.

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# DISCOVERY OF THE FAMILY BLEPHARICERIDAE (DIPTERA) IN CUBA, INCLUDING THE DESCRIPTION OF A NEW SPECIES

CHARLES L. HOGUE[1] AND GABRIEL GARCÉS G.[2]

**ABSTRACT.** A member of the dipterous family Blephariceridae (Blephariceridae, Apistomyiini) has been discovered on the island of Cuba. It is a new species, *Paltostoma palominoi,* from the Sierra Maestra, Santiago de Cuba Province. Although it shares some character states with *Paltostoma argyrocincta* and an unnamed species from Puerto Rico, its affinities are uncertain, with different stages bearing some similarities with both *Limonicola* and other special groups within *Paltostoma.* The larva, pupa, and adult male and female are described and figured.

**RESUMEN.** Se ha encontrado un miembro de la familia Blephariceridae de Diptera (Blephariceridae, Apistomyiini) de la isla de Cuba. Es una especie nueva, *Paltostoma palominoi,* de la Sierra Maestra, Provincia Santiago de Cuba. A pesar de que algunos caracteres establecen su relación con *Paltostoma argyrocincta* y una especie no nombrada de Puerto Rico, sus afinidades son inciertas, pués los diferentes estadios muestran similtudes parciales con *Limonicola* y unos grupos de especies de *Paltostoma.* Se describen, y muestran figuras de la larva, pupa, macho, y hembra.

## INTRODUCTION

Despite the considerable history of entomological research in Cuba, the family Blephariceridae was unknown until Garcés discovered a thriving population in the Sierra Maestra, Santiago de Cuba Province, in 1987 (Garcés et al., in press). The species proved to be new and is described here from material collected the following year.

Where not self-evident or labelled on figures herein, explanations for the terms used in this paper for morphological structures are explained by Hogue (1987; Hogue and Bedoya, in press). A new pupal character introduced below is the ratio of the anterior division of the body to the posterior division (HM/TA). The measurements are made along the dorsal midline; the anterior division (HM) from the front margin of the head to the rear of the scutum (scuto-metathoracic suture), and the posterior division (TA) from the front margin of the metathoracic tergite (scuto-metathoracic suture) to the terminus of the abdomen (Head–Mesothorax/meTathorax–Abdomen). All measurements in the description below are in millimeters.

## *Paltostoma palominoi* Hogue and Garcés, new species

### DESCRIPTION

**MALE** (Figs. 1–4, 7–10). Based on four teneral specimens (extracted from pupae, dissected, and mounted on slides) plus two mature specimens (including holotype), dissected and mounted on slides. *Coloration:* Indeterminable. Wing membrane hyaline. *Size:* A small blepharicerid. Measurements: wing length (N = 1) 3.5. Lengths of leg segments (N = 1 for femur–tarsus 1, N = 5 for tarsi 2–5):

| | | fore leg | mid leg | hind leg |
|---|---|---|---|---|
| femur | | 1.4 | 2.5 | 2.9 |
| tibia | | 2.3 | 2.7 | 3.1 |
| tarsus | 1 | 1.1 | 1.0 | 1.0 |
| | 2 | 0.51 (0.48–0.55) | 0.55 (0.50–0.58) | 0.51 (0.49–0.56) |
| | 3 | 0.34 (0.31–0.37) | 0.35 (0.30–0.38) | 0.32 (0.29–0.36) |
| | 4 | 0.19 (0.18–0.20) | 0.18 (0.17–0.19) | 0.18 (0.16–0.19) |
| | 5 | 0.22 (0.21–0.23) | 0.21 (0.20–0.24) | 0.21 (0.20–0.24) |

**Head** (Fig. 3). Semi-colocephalous type, dichoptic. Eyes disjunct dorsally, interocular distance about 0.3 head width; anterior eye margin entire. Mouthparts incompletely developed, proboscis short, labium length slightly less than head width; mandibles and hypopharynx completely absent; palpus very short, a single elongate segment, sensory pit absent. Antenna (Fig. 3) short (about same length as width of head), 14- (sometimes 13-) segmented, terminal segment sometimes partially fused, flagel-

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[1] 1. Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

[2] 2. Delegación Territorial, Academia de Ciencias de Cuba, Instituto de Ecología y Sistemática, Ave. Manduley, No. 308, Vista Alegre, Santiago de Cuba, Cuba.

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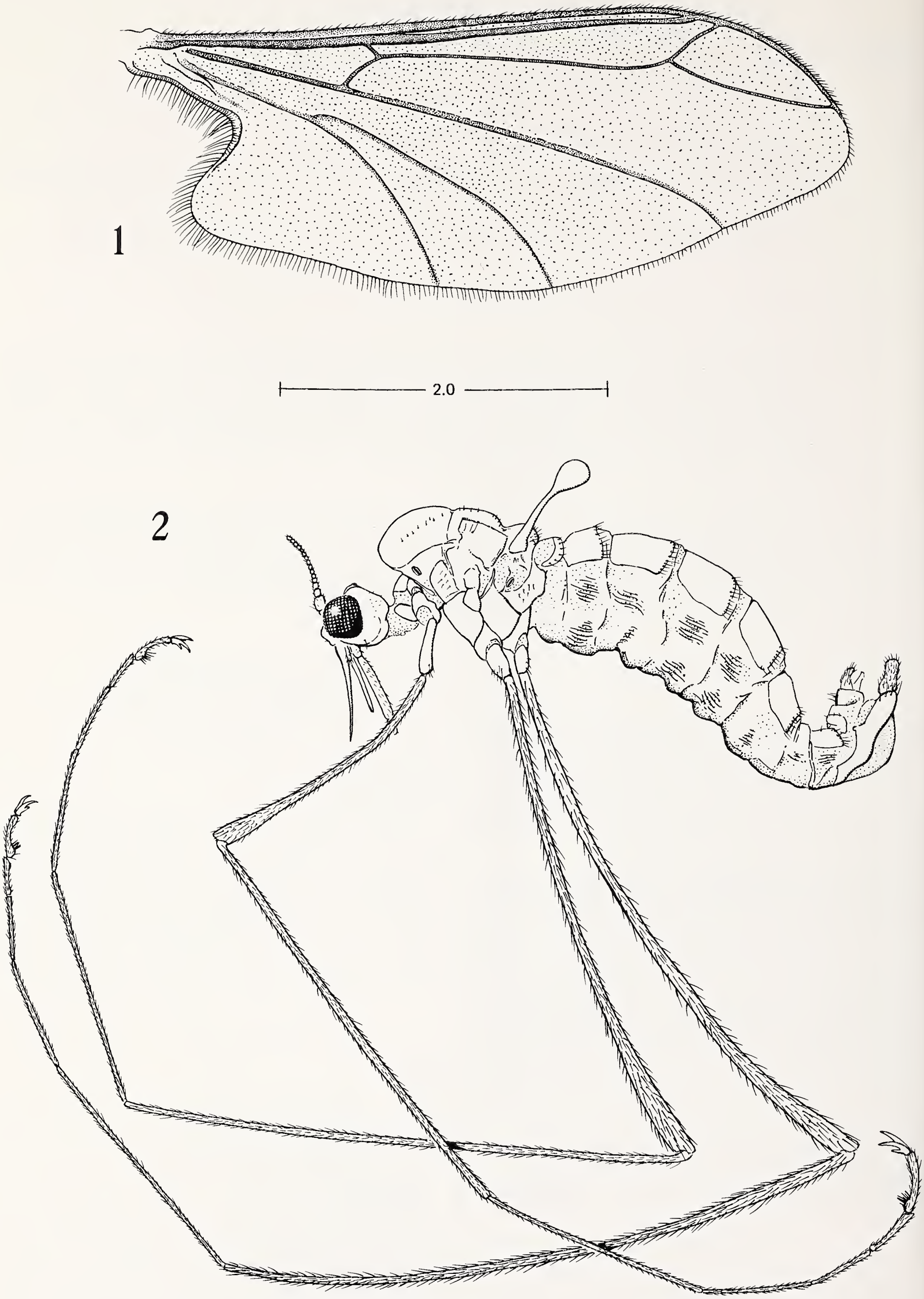
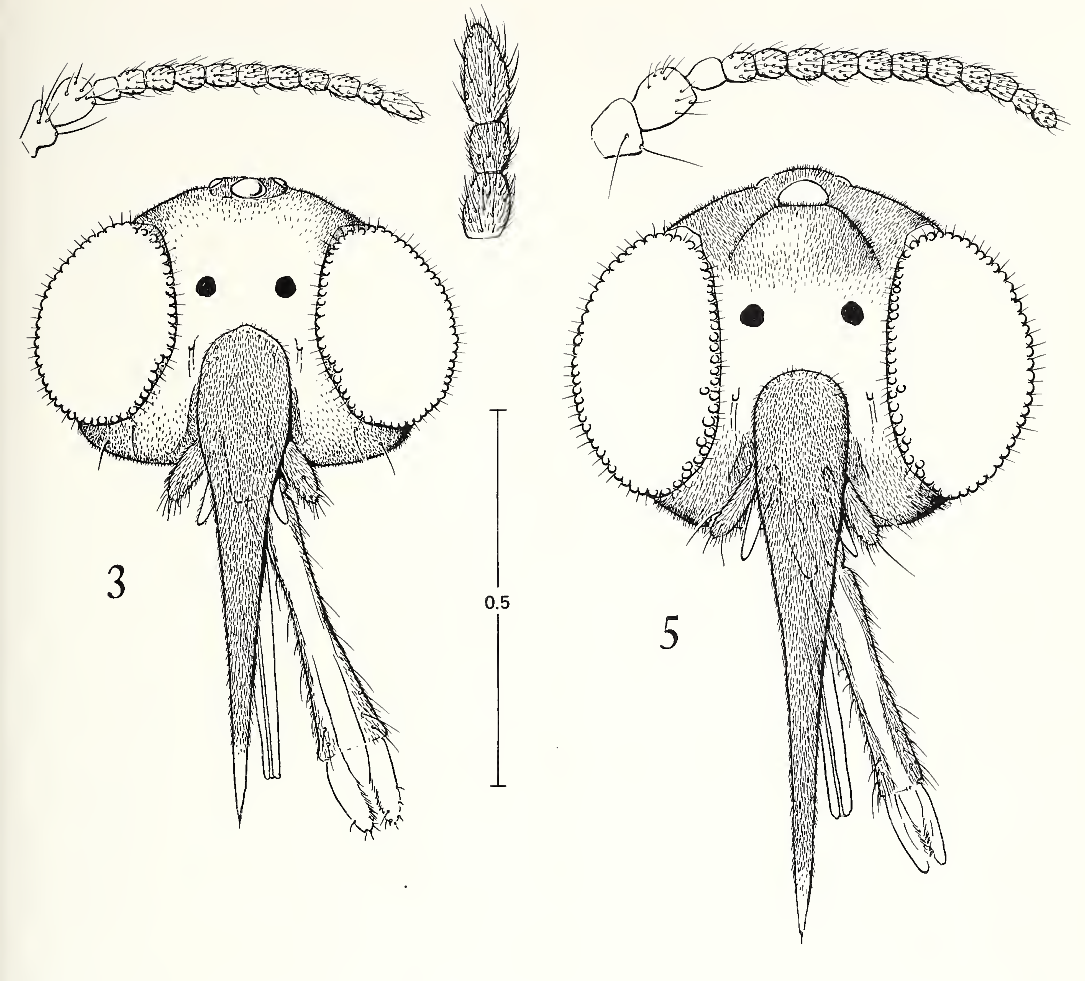


Figures 1, 2. *Paltostoma palominoi.* **1.** Right wing of male (dorsal view). **2.** Adult male (left lateral view).



**Figures 3–6.** *Paltostoma palominoi.* **3.** Head of male (frontal view) with antenna above (apical segments enlarged to right). **4.** Terminal tarsal segments of male; fore (upper), mid (center), hind (lower). **5.** Head of female (frontal view) with antenna above. **6.** Terminal tarsal segments of female (lateral view), arrangement as for male.

lar segments submoniliform, ultimate segment longer (1.6) than penultimate, penultimate segment slightly diminutive, proportions of apical three segments: 1.0–0.9–1.4.

*Sensilla.* Setiform groups on head capsule and mouthparts as follows: clypeals numerous, minute, basal; occipitals few (7–8), scattered; genals few (1–2); postgenals and labrals absent; labials and labellars numerous, scattered throughout.

**Thorax and Appendages** (Figs. 1, 2, 4). Wing venation as in Figure 1, typical of *Paltostoma.* Anal angle of wing slightly produced, a small lobe. Legs long and slender, hind leg slightly stouter than others. Tibial spurs 0–0–0. Progressive proportions of leg segments: fore leg 1.6–0.5–0.5–0.7–0.6–1.2, mid leg 1.1–0.4–0.6–0.6–0.5–1.2, hind leg 1.1–0.3–0.5–0.6–0.6–1.2; basitarsus short in relation to tibia in all legs (0.3–0.5), especially hind leg (0.3). Tarsomeres 5 similar on all legs, curved, with pollex (basal group of several heavy setae); claw sickle-shaped, with strong subbasal tooth.

*Sensilla.* Setiform groups on thoracic sclerites as follows: acrostichals few, anterior only; dorsocentral series complete; supraalars several (5–7), dorsal; prescutellars absent; scutellars numerous, generally distributed across sclerite, slightly more numerous laterad; preepisternals few (2–3), in ventral part; metapleurals several (5–7); suprametapleurals few (2–4).

**Terminalia** (Figs. 7–10). Genital capsule elongate. Cerci parallel to slightly divergent, a transverse sclerotization connecting bases; interlobular depression deep, broadly U-shaped; individual cercus elongate, slightly oblique, and curved gently ventrad. Inner arms of cerci convergent, apices widely separated. Walls of subanal pouch thin. Tegmen entirely soft and membranous, broadly rounded and finely spiculate apically, no medial recurved keel dorsally. Outer gonostylus large (length 0.8 width of genital capsule), an elongate, rectangular lobe, very slightly expanded and rounded apically. Inner gonostylus an elongate, porrect strap, apex projecting as a point laterally, inner margin and apex densely long-spiculate. Sperm sac broad, hemiovate, anteriorly spiculate on inner wall, outer wall with fine striae dorsally. Piston a large, pear-shaped sac with spicules on inner walls anteriorly; apodeme absent; vasa deferentia joining laterally, at narrowest point. Neither ventral plate nor lateral tines present. Aedeagal rods short, walls thick basally and internal canal evident basally.

*Sensilla.* Epandrium with several medium setiforms in a sparse transverse series. Cercus with numerous long setiforms generally, these more dense and longer medially. Setae of inner arm several to numerous (8–16), scattered basad, clustered distad. Outer gonostylus with medium setiforms general on ectal and ental surfaces, none concentrated into groups. Alveoliform sensilla of tergite X not apparent. Sternite X without apical setiforms.

**FEMALE** (Figs. 5, 6, 11). Based on four teneral specimens (extracted from pupae, dissected, and mounted on slides) plus two mature specimens (including allotype), dissected and mounted on slides. *Coloration:* Indeterminable. Wing membrane hyaline. *Size:* A small blepharicerid. Measurements: wing length (N = 1) 3.5. Lengths of leg segments (N = 1 for femur–tarsus 1, N = 5 for tarsi 2–5):

| | | fore leg | mid leg | hind leg |
|---|---|---|---|---|
| femur | | 1.0 | 2.0 | 2.4 |
| tibia | | 1.1 | 1.8 | 2.2 |
| tarsus | 1 | 0.5 | 0.8 | 0.9 |
| | 2 | 0.22 (0.18–0.25) | 0.36 (0.30–0.40) | 0.38 (0.30–0.46) |
| | 3 | 0.14 (0.11–0.18) | 0.20 (0.18–0.24) | 0.20 (0.18–0.23) |
| | 4 | 0.14 (0.09–0.14) | 0.13 (0.11–0.16) | 0.14 (0.11–0.16) |
| | 5 | 0.17 (0.14–0.19) | 0.17 (0.15–0.20) | 0.17 (0.17–0.18) |

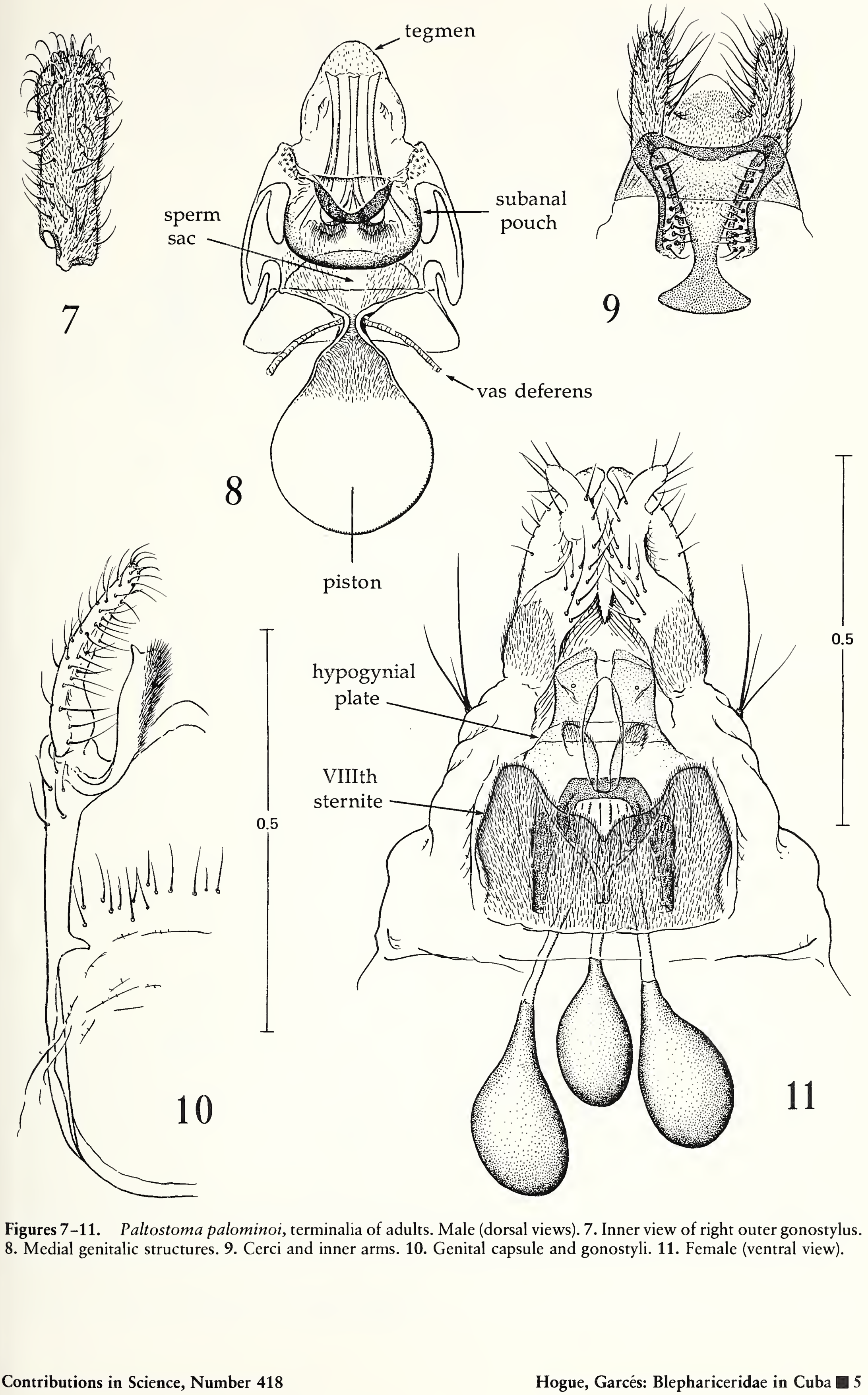
**Head** (Fig. 5). Virtually identical to that of male. Semi-colocephalous type, dichoptic. Eyes disjunct dorsally, interocular distance about 0.3 head width; anterior eye margin entire. Mouthparts incompletely developed, proboscis short, labium length slightly less than width of head; mandibles and hypopharynx completely absent; palpus very short, a single elongate segment, sensory pit absent. Antenna short (about same length as width of head), 14- (rarely 13-) segmented, some segments sometimes partially fused, flagellar segments submoniliform, ultimate segment equal to penultimate, proportions of apical three segments: 1.0–0.9–0.9.

*Sensilla.* Setiform groups on head capsule and mouthparts as follows: clypeals numerous, minute, basal; occipitals few (6–8), scattered; genals few (1–2); postgenals and labrals absent; labials and labellars numerous, scattered throughout.

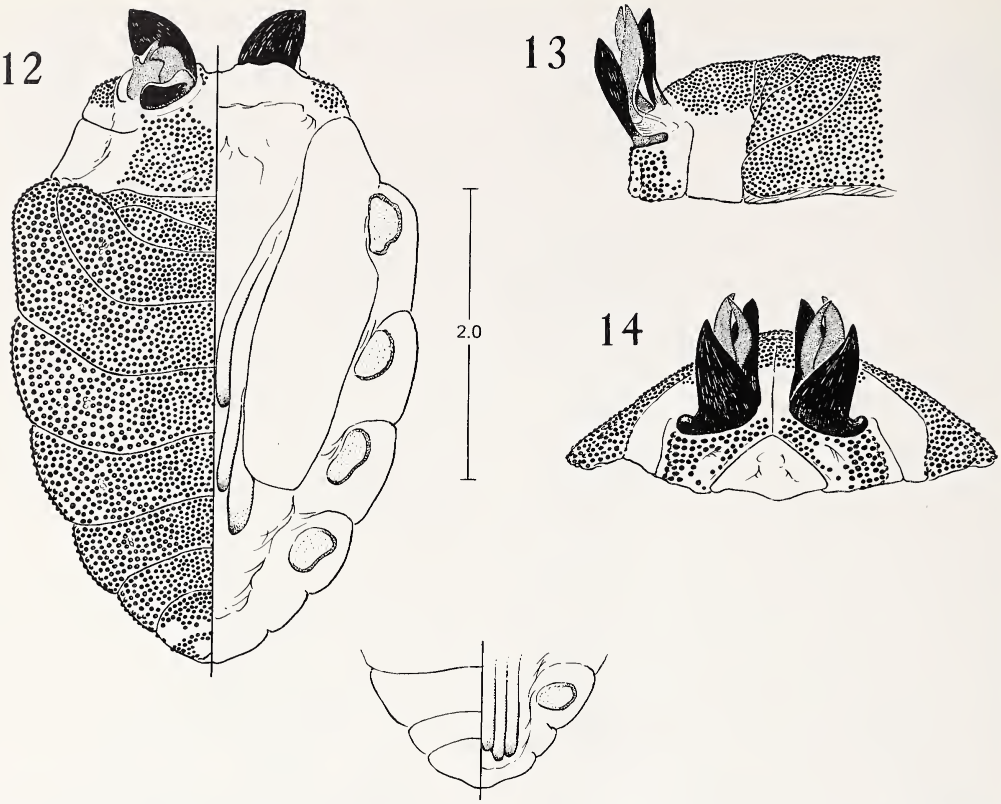
**Thorax and Appendages** (Fig. 6). Wing venation as in male. Anal angle of wing somewhat produced, a small lobe. Legs long and slender, femora incrassate, hind leg slightly stouter than others. Tibial spurs 0–0–0. Progressive proportions of leg segments: fore leg 1.1–0.4–0.5–0.7–1.0–1.2, mid leg 0.9–0.4–0.5–0.6–0.7–1.3, hind leg 0.9–0.4–0.4–0.5–0.7–1.2; tarsomeres 4 long in relation to 3 in all legs (1.0–0.7). Tarsomeres 5 similar in all legs, straight, with poorly developed pollex (basal group of only two to four heavy setae); claw sigmoid, simple (without subbasal tooth).

*Sensilla.* Setiform groups on thoracic sclerites as follows: acrostichals absent; dorsocentral series complete; supraalars several (6), dorsal; prescutellars absent; scutellars numerous, generally distributed across sclerite, slightly more numerous laterad; preepisternals several (8), general; metapleurals several (6–9); suprametapleurals few (4–5).

**Terminalia** (Fig. 11). Sternite VIII well sclerotized throughout, base broad; lateral margin slightly convex, medial depression moderately deep, broadly V-shaped, margin sinuate, internal sclerotization narrow, Y-shaped; lobe broad, with truncate apex. Hypogynial plate complex, base narrower than distance between lobes of sternite VIII; lobe undivided and smooth with broad neck, apex minutely spicu-



**Figures 7–11.** *Paltostoma palominoi*, terminalia of adults. Male (dorsal views). **7.** Inner view of right outer gonostylus. **8.** Medial genitalic structures. **9.** Cerci and inner arms. **10.** Genital capsule and gonostyli. **11.** Female (ventral view).



**Figures 12–14.** *Paltostoma palominoi,* pupa. **12.** Entire male, with posterior portion of female inset to lower right (dorsoventral views). **13.** Anterior portion (lateral view). **14.** Anterior portion (frontal view).

late; interlobular area reflexed dorsally to form an elongate capsule. Sternite IX well defined, stirrup-shaped; tergite IX undefined. Spermathecae three in number, all large, pear-shaped, with short necks; moderately well sclerotized, outers equal and somewhat larger than central; duct of central much shorter than outers.

*Sensilla.* Sternite VIII with several medium setiforms distributed generally over lobe.

**PUPA** (Figs. 12–14). **Integument.** Border terminate, underfolded and ventrally sclerotized anteriorly only. Papillose dorsally. Papillae general on abdominal and thoracic tergites and on disc of scutum; present on branchial sclerite, these large and more dense posteriad. Abdominal papillae evenly spaced, somewhat disperse, more so laterad than mediad. Individual papillae moderately large, on abdominal tergites larger laterad (mean diameter 25.2 microns), grading to slightly smaller mediad (mean diameter 21.4 microns); scutal papillae about average in diameter. Thoracic papillae smooth, rounded, oval convexities, abdominal papillae minutely spinulate.

**Size.** Small for family. Measurements: male (N = 14): body length 3.2 (2.8–3.5), width 2.0 (1.8–2.3); female (N = 15): body length 3.7 (3.4–4.1), width 2.4 (2.1–2.8). Male 0.7 size of female.

**General.** Outline shape oviform, thorax abruptly narrowed. L/W male = 1.6, female 1.5. Anterior division small in relation to posterior division (HM/TA: male = 0.35, female = 0.33). Shape in cross section subtriangular, dorsoventrally depressed; sides slightly inclined. Dorsal sclerites: cephalic sclerite triangular, flat. Branchial sclerite narrow, planate. Anterior margin of scutum gradually inclined. Suture separating metathoracic from abdominal tergite I, angulate medially. Abdominal tergites smoothly convex middorsally (no medial ridges or nodes); lateral margins entire.

**Branchiae.** Erect; anterior and posterior plates rigid and heavily sclerotized; inner plates thin and semi-membranous. In frontal aspect, anterior plates divergent, middle pair appressed and parallel, their apices often overlapping, hind pair parallel. Base of anterior plate expanded posterolaterad to form a small bullate ridge. Anterior and posterior plates triangular, with acute and slightly curved apices; middle plates elongate, curved, with acute apices.

**Ventral Sclerites.** Cases of head appendages obscure; leg cases of female very unequal in length, apices uneven; apices of leg cases of male coterminate. Four adhesive disks (on abdominal segments III–VI).

**LARVA** (Fig. 15). **General.** Body form subonis-

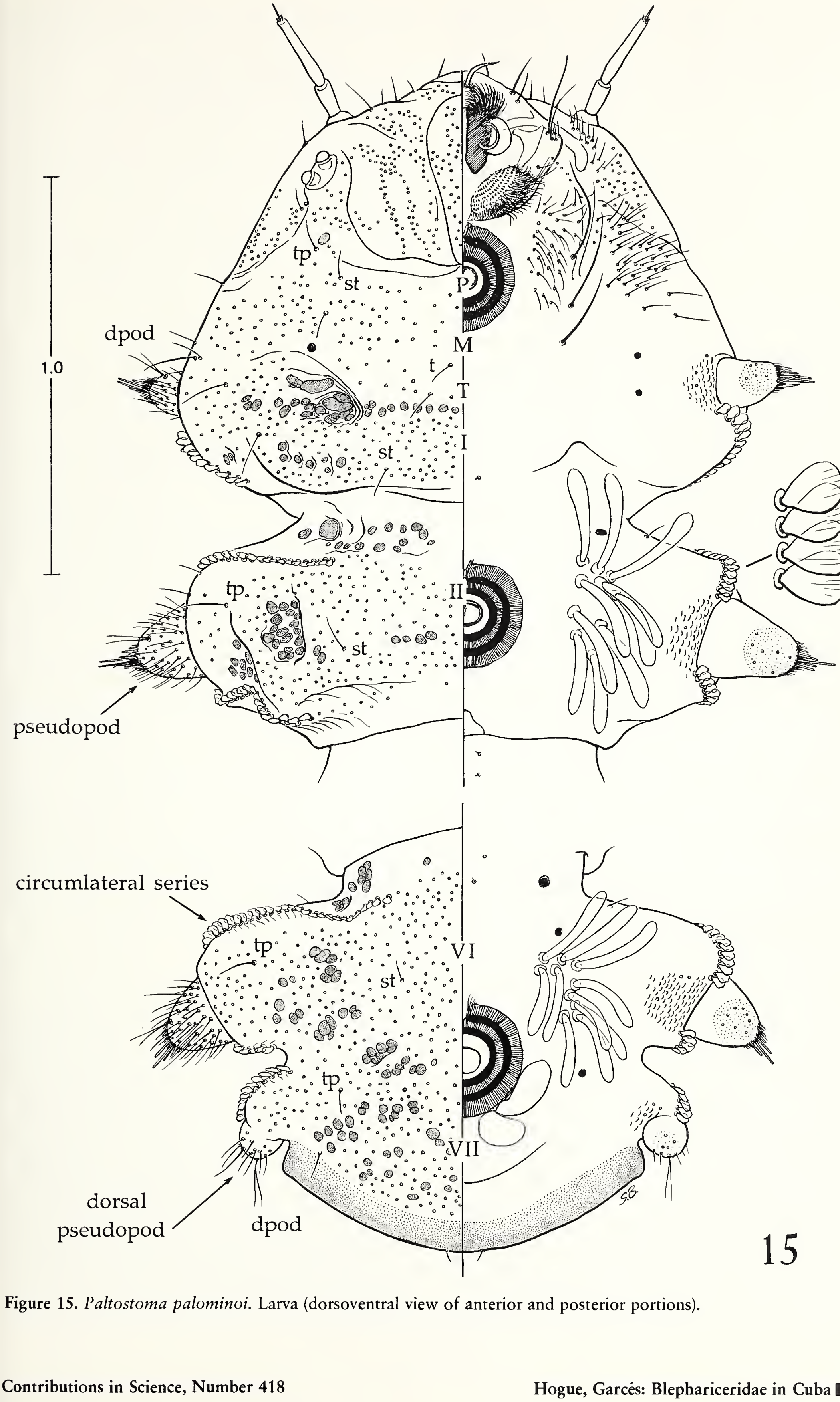


**Figure 15.** *Paltostoma palominoi.* Larva (dorsoventral view of anterior and posterior portions).

ciform. Medial elevated zones of abdominal segments not well defined. Outline shape of anterior division subhexagonal.

**Integument.** Dorsum moderately well sclerotized. Corrugations distinct, mostly irregular. Venter with area at bases of pseudopods lightly imbricate.

**Coloration.** Trunk pigmentation even, light brown; sclerotized portions pale brown, terminal border lightly pigmented.

**Size.** Medium for the family. Measurements (N = 11): body length 5.1 (4.5–5.7); head capsule width 1.2 (1.1–1.3); antennal segment lengths, basal 0.10 (0.08–0.11), apical 0.21 (0.20–0.24).

**Head.** Two distinctly separated lenses in eye. Antenna short, segment proportions 1.0–2.1.

**Trunk.** Dorsum of abdominal segments I–VI more or less evenly rounded, without convexities, projections, or large plates; numerous small plates on anal division and dorsolaterally on abdominal segments.

**Anal Division.** Dorsal pseudopod small, a nub, directed inward slightly. Terminal incision shallow. Terminal lobe broadly arcuate.

**Primary Sensilla** (medium setiforms unless otherwise described). tM–T oblique, tM medial to tT. stM–T slightly medial to line between tpP and tpM; stI–VI distant from tI–VI, tI–VI indiscernible, no PT tubercle. stVII and inner tp proximate. Inner tpP anteromedial to spiracle; inner tpI medial to homolog on M; inner tpII–VI set well anteriad. Outer tpI–VI indiscernible. Terminal setae 1–1, short chaetiforms.

**Dorsal Modified Sensilla.** Consist of minute, variously shaped projections (apparently oviform but barely visible and only slightly exceeding alveoli) in linear series and patches on head sclerites, and generally and evenly spaced on body integument. Circumlateral series complete, of foliose sensilla. Sensilla of pseudopods setiform generally, several truncate chaetiforms apically. Background field of fine setiforms absent.

## SPECIMENS EXAMINED

TYPES. HOLOTYPE male (dissected and mounted on slides nos. CLH 89-38H, 89-38B, 89-38W, and 89-38M); ALLOTYPE female (dissected and mounted on slides nos. CLH 89-39H, 89-39B, 89-39W, and 89-39F). Deposited in Academia de Ciencias de Cuba, Santiago de Cuba. 1 male, 1 female PARATYPES [dissected and mounted on slides nos. CLH 89-5B, 89-5W, 89-5H, 89-5M (male), 89-6B, 89-6W, 89-6H, and 89-6F (female), from alcohol]. Deposited in Los Angeles County Museum of Natural History. 4 male, 4 female PARATYPES (teneral, extracted from pupal skins, dissected, and mounted on microscope slides). Deposited one pair each in British Museum of Natural History, London; United States National Museum, Washington, D.C.; Zoological Institute, Academy of Sciences, Leningrad; American Museum of Natural History, New York: CUBA, *Santiago de Cuba Province*, Sierra Maestra, Río Palma Mocha, 700 meters, 23–24 February 1988, Gabriel Garcés.

ADDITIONAL SPECIMENS. 8 pharate male pupae, 7 pharate female pupae, 10 prepharate pupae, 120 larvae: same data as types. Deposited in British Museum of Natural History, London; United States National Museum, Washington, D.C.; Zoological Institute, Academy of Sciences, Leningrad; American Museum of Natural History, New York; Los Angeles County Museum of Natural History; Academia de Ciencias de Cuba, Santiago de Cuba.

## DIAGNOSIS AND AFFINITIES

In northern South America and the Caribbean only the genera *Paltostoma* and *Limonicola* are recognized presently (Hogue and Bedoya, in press). Although it is still in a chaotic taxonomic state, with limits undefined, *Paltostoma* receives the new species at this time on the basis of the following synapomorphies: free inner gonostylus of the male terminalia (fused to aedeagal guide in *Limonicola*), elongate mouthparts of the adults of both sexes (vestigial in *Limonicola*), and well-developed circumlateral series of specialized dorsal setae in the larva (absent in *Limonicola*). We make this combination in spite of several similarities with *Limonicola:* male terminalia with large sperm sac and expansive ventral bridge, tendency toward colocephaly in the adult heads, pupa with base of anterior lamella expanded and subbullate, integument at base of pseudopods ventrally ornamented in larva rather than setose, and dorsal pseudopod VII moderately free of the terminal lobe.

In the Neotropical Region there are several species groups of *Paltostoma* that are known to Hogue but not yet formally recognized; their phyletics are still being considered. On the basis of overall similarity, the new species is not closely related to any of those on the mainland, certainly not to that containing the type of the genus from South America or to those of Mexico or Central America, which have either lateral tines or a ventral plate in the male terminalia. The shape of the terminal lobe of the larva is of the same type as the species of Puerto Rico (*Paltostoma argyrocincta* Curran, 1927, and undescribed species), and the structures of the male terminalia are somewhat similar to those of that species (lack of ventral plate or lateral tines, simple broad aedeagal rods, broad sperm sac with armature). Also, the lateral entry of the vasa deferentia and spiculate inner gonostyli occur in the Cuban and Puerto Rican males and appear to be synapomorphies relating them. Thus, the new species seems most likely to have its sister species in Puerto Rico. (No blephariceridis known from intervening Hispaniola despite an intensive search in suitable habitats there by Hogue in March of 1987.) *Paltostoma palominoi* clearly belongs to a distinct phyletic line from the *P. schineri* group, which occupies the Lesser Antilles.

*Paltostoma palominoi* is readily recognized by well-defined characteristics in all stages: the most distinctive features in the male terminalia are the very large saccate piston with laterally emerging vasa deferentia and spiculate inner gonostylus. The lobes of the hypogynial plate in the female terminalia are uniquely simple, without either ornamentation or a secondary ventral sublobe. The proportions of the pupa are distinctive, the length of anterior division shorter relative to the posterior than in other species (HM/TA = 0.35; usually >0.5 in South American *Paltostoma*). The combination of the long antenna, imbricate integument ventrally at the base of the pseudopods, and general field of minute dorsal sensilla identifies the larva.

## ZOOGEOGRAPHY

Blephariccrids are extremely poor dispersers with virtually no ability to cross large expanses of ocean. Thus, the occurrence of related species on Cuba and Puerto Rico suggests that these islands were connected, or located very close to each other, in the past. Also implied by this distribution is a connection of these islands with mainland South or Central America, because of the almost certain origin of the island species from continental ancestors.

These facts are in support of the "vicariance model" of Caribbean biogeography and recent plate tectonic studies of the area (Hedges, 1982). Furthermore, the new Cuban species' apparent restriction to the eastern end of the island lends some support to the hypothesis of separate origin of this portion from the larger central-western portion (Pregill, 1981). [A similar binary origin and subsequent accretion of the two parts is proposed for Hispaniola (Durham, 1985).] Isolation of this portion is also suggested by its recognition as a distinct "natural region" of high endemicity [e.g., for Trichoptera (Botosaneanu, 1977)].

## ECOLOGY

Río Palma Mocha is located in a deep, well-forested valley between Pico Turquino and Palma Mocha Mountain, in the Sierra Maestra. The river heads on the north side of the former (highest peak in Cuba) and flows 13.5 km south from the cordillera to Sierra Maestra beach on the coast.

The immatures were found in typical blepharicerid microhabitats, the larvae only in shallow, clean, pollution-free water flowing rapidly over the vertical upper portions of large stones (30–60 cm diameter); the pupae were most numerous near the brinks of the same falls. Immatures were absent from submerged stones at the base of the falls. Water temperature at the collecting site ranged from 18 to 20°C. No free-flying adults were seen, but four mature adult specimens (including the holotype) were collected from a spider's web situated between rocks at the edge of the stream.

## ETYMOLOGY

The species is named in honor of José Palomino Oliva, a kind and hard-working Cubano, who has contributed in many ways to the development of studies on the flora and fauna of the Río Palma Mocha area of the Sierra Maestra.

## REMARKS

Association of the stages as described here is certain, determined by the "ontogenetic method" (examination of the pharate succeeding stage within the skin of the preceding; Hogue and Bedoya, in press). By analogy with the situation in Puerto Rico, a much smaller island than Cuba, the possibility exists that additional species of the family may be found here.

## ACKNOWLEDGMENTS

We are grateful to Srs. José Palomino and Fernando E. Vera, who aided greatly in the collection of the material. We also acknowledge our indebtedness to our respective institutions for making these investigations possible. A portion of this study was supported by a grant to Hogue from the Systematic Biology Program of the U.S. National Science Foundation (BSR 8415044).

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# CONTRIBUTIONS IN SCIENCE

## BIOSTRATIGRAPHY OF UINTAN AND DUCHESNEAN LAND MAMMAL ASSEMBLAGES FROM THE MIDDLE MEMBER OF THE SESPE FORMATION, SIMI VALLEY, CALIFORNIA

THOMAS S. KELLY

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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# BIOSTRATIGRAPHY OF UINTAN AND DUCHESNEAN LAND MAMMAL ASSEMBLAGES FROM THE MIDDLE MEMBER OF THE SESPE FORMATION, SIMI VALLEY, CALIFORNIA

THOMAS S. KELLY[1]

**ABSTRACT.** The Sespe Formation is composed of middle Eocene to upper Oligocene continental strata exposed along the northern side of Simi Valley, Ventura County, California. In this area, the Sespe Formation is divided into three (lower, middle, upper) members. The lower part of the middle member has yielded middle and late Eocene land mammal assemblages. A general section of this part of the formation consists of 22 sandstone (SS) beds, each overlain by a claystone (CS) bed. In ascending order, these beds are numbered 1 through 22.

Three late Eocene local faunas were previously recognized from the lower part of the middle member: the late Uintan Tapo Canyon and Brea Canyon Local Faunas and the Duchesnean Pearson Ranch Local Fauna. However, a fourth local fauna can be recognized. Each local fauna is characterized by a distinctive suite of assemblages stratigraphically restricted to a particular interval within the section. The Tapo Canyon Local Fauna, stratigraphically lowest in the middle member, includes the assemblages from beds CS1 through the lower part of SS2. The Brea Canyon Local Fauna consists of the assemblages from beds CS2 through CS6 and lies about 50 to 100 m stratigraphically above the Tapo Canyon Local Fauna. The Pearson Ranch Local Fauna as recognized by previous workers in Simi Valley actually consists of two stratigraphically and taxonomically distinct local faunas: the Strathern Local Fauna (new) and the Pearson Ranch Local Fauna (restricted). The latest Uintan or earliest Duchesnean Strathern Local Fauna is comprised of the assemblages from beds CS8 through CS14 and lies about 200 to 300 m above the Tapo Canyon Local Fauna. The early Duchesnean Pearson Ranch Local Fauna is redefined to include only the fossil assemblages from the upper part of bed SS15 through bed SS22 and lies about 315 to 475 m above the Tapo Canyon Local Fauna.

New Uintan taxa and occurrences recorded from Simi Valley are *Macrotarsius roederi* n. sp.; *Leptoreodon pusillus* Golz, 1976; *Leptoreodon stocki* n. sp.; and *Protylopus*? sp., cf. *P.*? *robustus* Golz, 1976. New Duchesnean taxa and occurrences recorded from Simi Valley are *Leptoreodon* sp., cf. *L. pusillus* Golz, 1976; *Leptoreodon stocki* n. sp.; and *Rapamys* sp. indet.

## INTRODUCTION

The Sespe Formation, which is exposed along the north side of Simi Valley, Ventura County, California, is one of the few stratigraphic sequences on the Pacific Coast of North America to produce middle and late Eocene land mammal assemblages. The most fossiliferous outcrops in Simi Valley are present in the Brea Canyon area, which includes lower Alamos and Brea Canyons and the unnamed canyon between Alamos and Brea Canyons (Fig. 1).

The Sespe Formation was first extensively investigated during the 1930's by parties from the California Institute of Technology (CIT), Pasadena, under the direction of Chester Stock. In a series of papers, Stock (1932, 1934b, 1935a, 1936a,b, 1939) described many new species and defined two faunas—the Pearson Ranch Fauna and the Tapo Ranch Fauna [= combined Tapo Canyon and Brea Canyon Local Faunas of Golz (1976)]. The CIT collection

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[1] Museum Associate, Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

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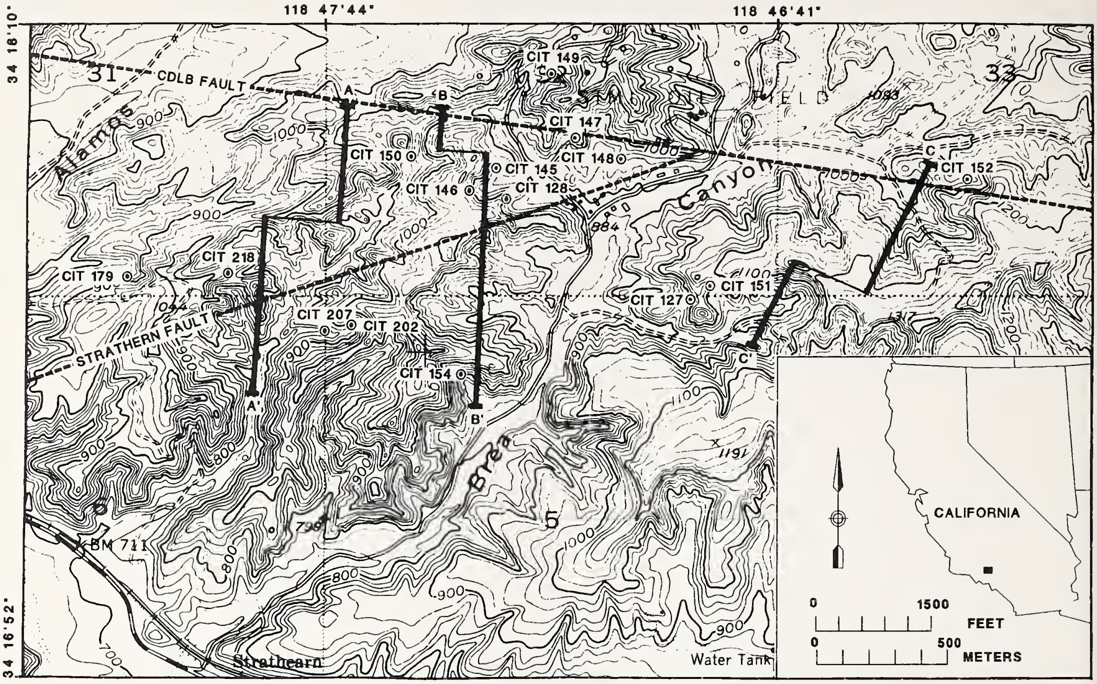

**Figure 1.** Map of Brea Canyon area showing locations of Strathern and Cañada de la Brea faults, key LACM(CIT) vertebrate fossil localities, and measured sections. Base map: U.S.G.S. 7.5 minute, Simi, Calif. quadrangle (scale 1:24,000), 1951, photorevised 1969.

was later transferred to the Natural History Museum of Los Angeles County (LACM), where it is presently housed. Since then, parties from the LACM and the University of California Museum of Paleontology (UCMP) have discovered additional localities in Simi Valley.

Only general summaries of the stratigraphic relations of the LACM(CIT) localities have been published (Stock, 1932; Golz, 1976; Golz and Lillegraven, 1977). Many localities in the unnamed canyon between Brea and Alamos Canyons, including LACM(CIT) locs. 150, 150.5, 202, 202E, 200W, and 207, were destroyed by the Simi Valley Landfill. These localities produced most of the specimens comprising the Brea Canyon and Pearson Ranch Local Faunas. Rapid urban development north of the Simi Valley Freeway (California 118) at the entrance to Brea Canyon is threatening many additional localities. Because of the importance of the land mammal assemblages from the Sespe Formation in Simi Valley and the continuing loss of fossil-bearing exposures, the present study was begun in the spring of 1977 to recover fossil remains and stratigraphic data that might otherwise have been lost to earth-moving activities. As the result of 11 years of field investigation, several hundred new specimens were recovered, all of the LACM(CIT) localities were relocated or their stratigraphic horizons identified, 34 new localities (LACM locs. 5616 through 5649, 5660) were discovered in Brea Canyon, and five new localities (LACM locs. 5611 through 5615) were recorded from the adjacent lower Alamos Canyon.

The goals of the study, described herein, are 1) to clarify the stratigraphic relations of the LACM(CIT), LACM, and UCMP localities; 2) to taxonomically and stratigraphically define the land mammal assemblages from the Sespe Formation in Simi Valley; and 3) to correlate the Uintan and Duchesnean assemblages from Simi Valley with other middle and late Eocene land mammal assemblages in California, Texas, Utah, and Wyoming.

## METHODS AND MATERIALS

As part of the present study, exposures of the Sespe Formation in Simi Valley were prospected for identifiable fossils, and each fossiliferous horizon was traced to adjacent outcrops. The locations of the LACM(CIT) localities were determined by 1) a review of the original locality descriptions in the CIT locality catalog and of photographs taken during the CIT field investigations (Sespe Excavations 1933, catalog and photographs now filed in the LACM archives), 2) examination of aerial photographs of the area, and 3) subsequent field investigation. In some cases, the location of a fossil locality was confirmed by the discovery of the original marking post in the field.

Stratigraphic sections were measured to the nearest 0.25 m with a Jacob's staff. Correlation of beds from section A-A' (west side of the Simi Valley Landfill) to section B-B' (west side of Brea Canyon) was accomplished by tracing key marker beds in the field and using the detailed geologic map prepared by Emcon Associates (1986). The contact between the lower and middle members of the Sespe Formation as defined by Taylor (1983, fig. 3) is used herein.

Statistical tests followed the format recommended by Simpson *et al.* (1960) and were run using computer programs compiled by Peters (1971) and Poole and Borchers (1979). A 95% or greater level of confidence was considered to represent a significant difference between samples, and all Student's t-tests were two-sided.

Potassium-argon dates cited in this report were recalculated using the new constants proposed by Steiger and Jager (1978) and the conversion factors presented by Dalrymple (1979).

Measurements of large teeth were made to the nearest 0.1 mm with a vernier caliper, and those of smaller teeth were made to the nearest 0.01 mm with an AO optical micrometer. All measurements are in millimeters, and all teeth were measured at their greatest dimensions. All metric abbreviations, dental formulae, and terminology follow standard usage.

Institutional acronyms are as follows:

CIT—California Institute of Technology
LACM—Natural History Museum of Los Angeles County
LACM(CIT)—California Institute of Technology locality number, files and specimens now held by LACM; CIT abbreviation for localities used in figures
RV—UCR vertebrate fossil locality
TMM—Texas Memorial Museum
UCR—University of California, Riverside
UCMP—University of California Museum of Paleontology
V—UCMP vertebrate fossil locality

Abbreviations are as follows:

CDLB—Cañada de la Brea
CS—claystone
ft—foot
K-Ar—potassium-argon
Lat.—latitude
loc.—locality
Long.—longitude
Ma—megannum (million years before present)
NALMA—North American Land Mammal Age
SS—sandstone

Abbreviations of anatomical terms are as follows:

A-P—anteroposterior
ANT—anterior
L—left
POST—posterior
R—right
TAL—talonid
TR—transverse
TRI—trigonid

## GEOLOGIC SETTING

The northern side of Simi Valley contains over 7100 m of upper Cretaceous to Pleistocene marine and nonmarine strata and minor submarine volcanics (Squires and Filewicz, 1983). The upper middle Eocene to upper Oligocene nonmarine Sespe Formation in Simi Valley consists of 1656 m of sandstone, conglomerate, and mudstone (Taylor, 1983).

Previous workers divided the Sespe Formation in Simi Valley into three (lower, middle, upper) members (Stock, 1932; Taylor, 1983; Mason, 1988). The lower member of the Sespe Formation rests unconformably on the lower middle Eocene marine Llajas Formation, and the upper member interfingers with the overlying upper Oligocene to lower Miocene marine Vaqueros Formation (Lander, 1983). The members have gradational contacts with each other (Taylor, 1983).

The middle member is composed of alternating tabular beds of structureless yellow to gray sandstone and mottled red and green claystone, interpreted by Taylor (1983) to represent a meandering-river flood-basin facies. Taylor (1983) determined that the sand comprising the sandstone beds was deposited by sheet floods at maximum flood-stage, and the clay composing the claystone beds was deposited from suspension during waning flood-stage or as flood-basin deposits. Calcrete nodules are present in some claystone beds indicating partial pedogenesis (Taylor, 1983). The sandstone and claystone beds have marked horizontal continuity in the Brea Canyon area and can be traced between widely separated exposures.

Two north-dipping reverse faults, the Strathern and Cañada de la Brea (CDLB) faults (Fig. 1), are present in the Brea Canyon area (Taylor, 1983; Kimmel *et al.*, 1983). Well log data from the Unocal CDLB #7 and CDLB #14 wells in Brea Canyon indicate strata along the CDLB fault are offset vertically by approximately 262 m (860 ft) with the north side up, and strata along the Strathern fault are offset vertically by approximately 46 to 55 m (150 to 180 ft) with the south side up (Kimmel *et al.*, 1983). These well log data also indicate the strata between the faults comprise a down-dropped fault block, with approximately 46 to 55 m of section removed just above the Strathern fault and approximately 262 m of section repeated above the CDLB fault (Figs. 2, 3).

## MEASURED SECTIONS

Three composite sections were measured and their beds correlated (Figs. 1, 3). Section A-A′ begins at the CDLB fault on the west side of the Simi Valley Landfill (west side of unnamed canyon between Brea and Alamos Canyons) and traverses southward and down section to the contact between the lower and middle members near the landfill entrance. Section B-B′ begins at the CDLB fault between LACM(CIT) locs. 145 and 150 and traverses southward along the west side of Brea Canyon (west Brea Canyon) down section to the contact between the lower and middle members, stratigraphically below LACM(CIT) loc. 154. Section C-C′ begins just above the CDLB fault in the vicinity of LACM(CIT) loc. 152 and traverses southwestward down section to the contact between the lower and middle members

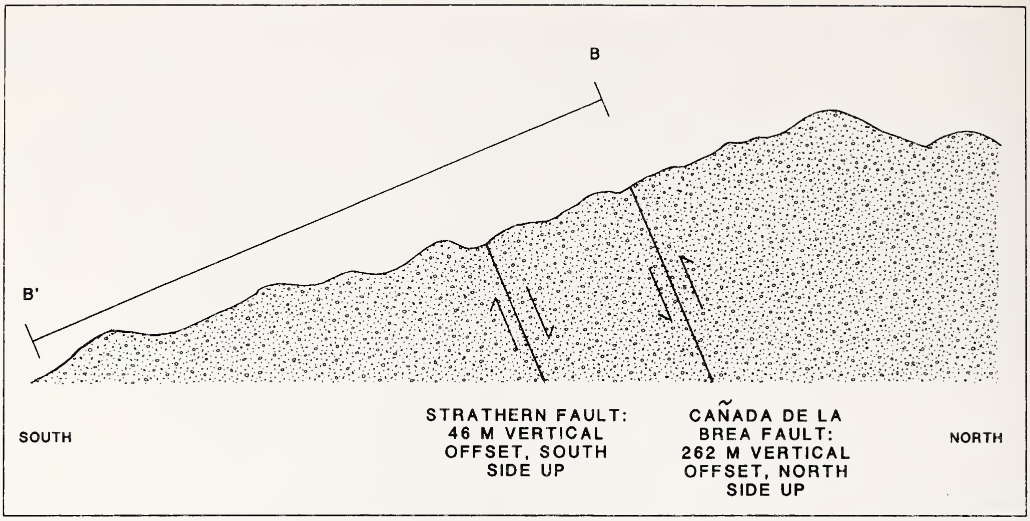
B
B'
SOUTH
STRATHERN FAULT: 46 M VERTICAL OFFSET, SOUTH SIDE UP
CAÑADA DE LA BREA FAULT: 262 M VERTICAL OFFSET, NORTH SIDE UP
NORTH

**Figure 2.** Stratigraphic relationships of beds between Strathern and Cañada de la Brea (CDLB) faults in area of section B-B′ (see Fig. 1). Strata along Strathern fault offset vertically approximately 46 to 55 m (150 to 180 ft) with south side up; strata along Cañada de la Brea fault offset vertically approximately 262 m (860 ft) with north side up. Strata between faults comprise a down-dropped fault block, with approximately 46 to 55 m (150 to 180 ft) of section missing above Strathern fault and approximately 262 m (860 ft) of section repeated above Cañada de la Brea fault.

in a tributary extending eastward from Brea Canyon (east Brea Canyon).

A general stratigraphic section of the lower part of the middle member in the Brea Canyon area (Fig. 4) was constructed from the three measured sections (Fig. 3). The general section consists of 22 major structureless sandstone (SS) beds, each overlain by a mottled claystone (CS) bed and numbered, in ascending order, 1 through 22 (Fig. 4).

Sections A-A′ and B-B′ were correlated directly by tracing 23 key beds between these sections in the field. Accurate correlation of sections B-B′ and C-C′ is based on tracing beds SS7 and SS8 across Brea Canyon from the roadcut in west Brea Canyon to the stream bank in the canyon floor and into east Brea Canyon. Moreover, the contact between the lower and middle members is present in sections B-B′ and C-C′.

The sandstone beds exhibit distinct weathering characteristics that allow correlation across areas of thick chaparral cover, even when the interbedded claystone beds become thin or discontinuous. However, some sandstone beds can change in thickness or lithology over short distances. For example, in the canyon that contains LACM(CIT) loc. 145, bed SS17 varies laterally from a 10-m-thick, yellowish-buff sandstone that weathers into vertical columns to a 5-m-thick, coarse-grained, clayey, structureless, light-gray sandstone, and then to a 6-m-thick, coarse-grained yellowish-gray sandstone.

It cannot be determined if the discontinuous claystone beds were deposited during the waning stage of the same or different flood events; however, their presence at the same stratigraphic levels over great distances suggests they represent isochronous events.

## VERTEBRATE FOSSIL LOCALITIES

Previous workers determined the stratigraphic positions of the vertebrate fossil localities in the Sespe Formation based on their distances above the base of the formation (Stock, 1932; Mason, 1988). Kelly and Lander (1988) noted that inaccuracies in the determination of the relative stratigraphic positions of fossil localities can occur when these determinations are based on distances of localities above or below a stratigraphic datum, such as the top or base of a formation. These inaccuracies result from variation in the thicknesses of individual beds along strike. Such variation occurs in the Brea Canyon area. For example, in east Brea Canyon the sequence consisting of beds SS1 through SS7 in the vicinity of LACM(CIT) loc. 127 is about 40 m thinner than the same sequence in west Brea Canyon.

To avoid such inaccuracies, the bed that produced each fossil locality was determined and traced laterally to other exposures. This process allowed documentation of the stratigraphic levels of most of the fossil localities to be accurately placed within the general section (Fig. 4); however, the stratigraphic positions of a few localities can only be estimated. LACM(CIT) loc. 149 lies above the CDLB fault in a part of the section that is repeated below the fault. Based on lithologic similarities and vertical displacement along the fault, the stratigraphic position of LACM(CIT) loc. 149 appears to be in bed CS8 (Fig. 4). The bed that contains LACM (CIT) loc. 152, which is also in strata repeated above the

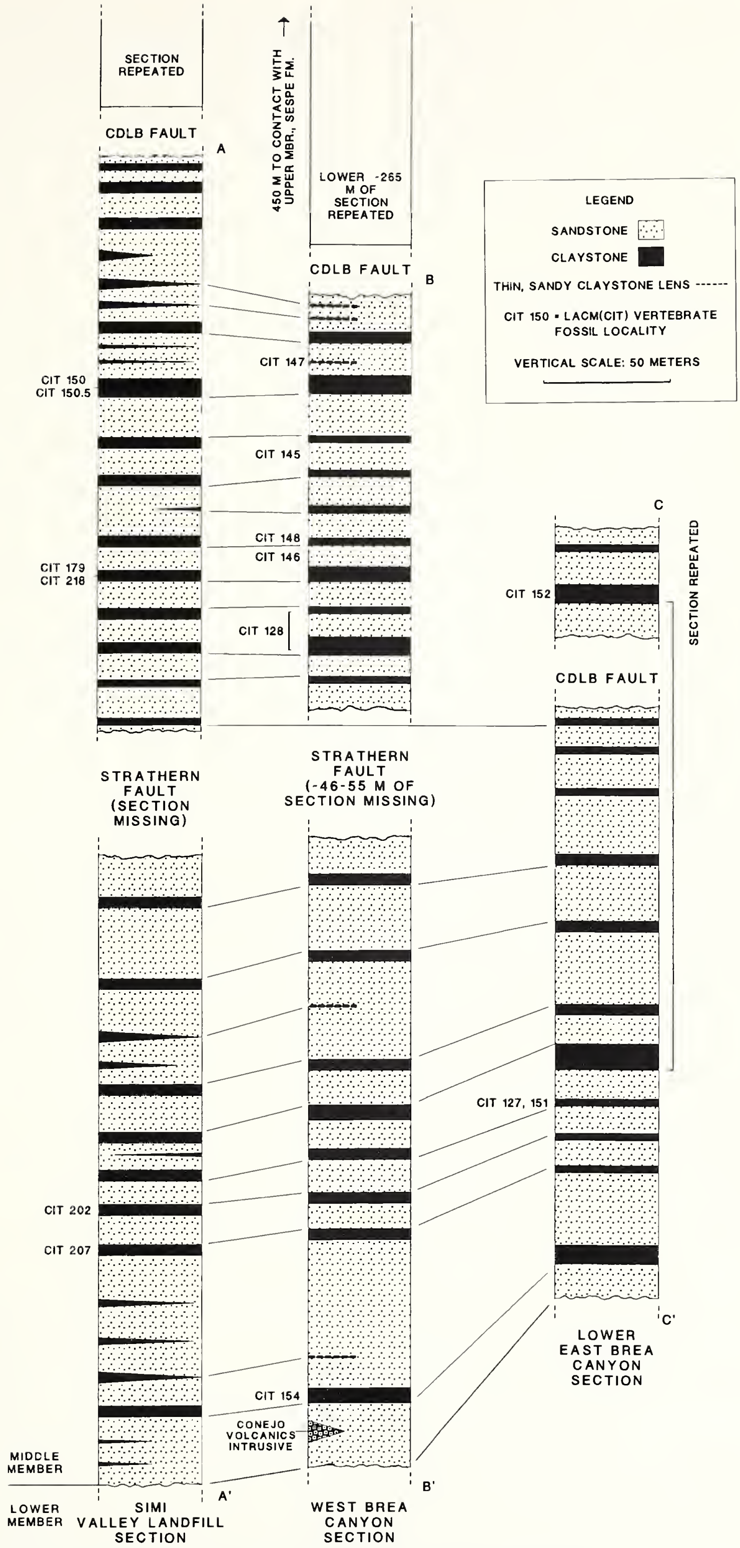
SECTION REPEATED
CDLB FAULT
A
450 M TO CONTACT WITH UPPER MBR., SESPE FM.
LOWER -265 M OF SECTION REPEATED
CDLB FAULT
B
LEGEND
SANDSTONE
CLAYSTONE
THIN, SANDY CLAYSTONE LENS ------
CIT 150 • LACM(CIT) VERTEBRATE FOSSIL LOCALITY
VERTICAL SCALE: 50 METERS
CIT 150
CIT 150.5
CIT 147
CIT 145
CIT 148
CIT 146
CIT 179
CIT 218
CIT 128
C
SECTION REPEATED
CIT 152
CDLB FAULT
STRATHERN FAULT (SECTION MISSING)
STRATHERN FAULT (-46-55 M OF SECTION MISSING)
CIT 127, 151
CIT 202
CIT 207
CIT 154
CONEJO VOLCANICS INTRUSIVE
MIDDLE MEMBER
LOWER MEMBER
A'
B'
C'
SIMI VALLEY LANDFILL SECTION
WEST BREA CANYON SECTION
LOWER EAST BREA CANYON SECTION

**Figure 3.** Correlation of sections A-A′, B-B′, and C-C′ in lower part of middle member of Sespe Formation in Simi Valley and stratigraphic positions of key LACM(CIT) vertebrate fossil localities.

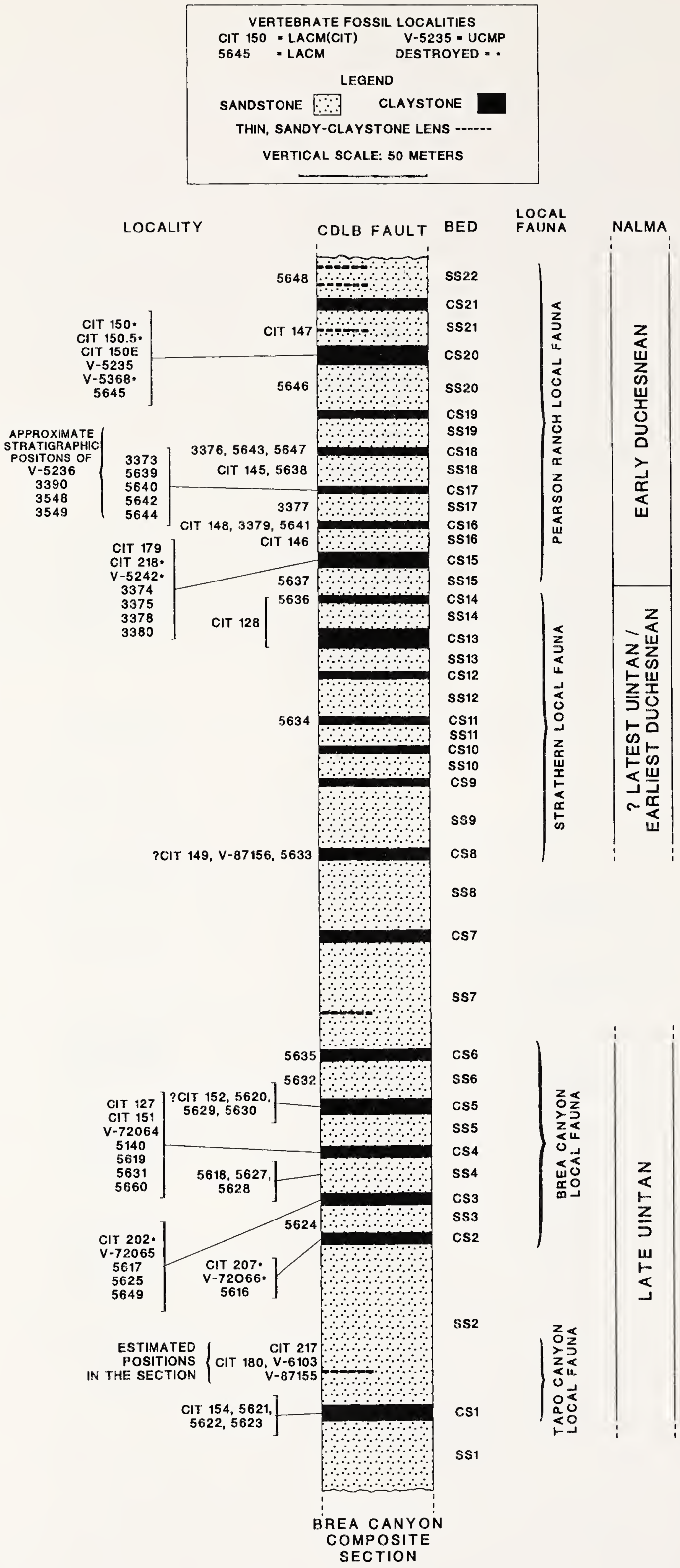

Figure 4. Generalized stratigraphic section of lower part of middle member of Sespe Formation in Brea Canyon area, based on sections A-A′, B-B′, and C-C′ (see Fig. 3) and showing stratigraphic positions of vertebrate fossil localities and local faunas.

CDLB fault, is correlated with bed CS5 on the basis of similar lithology. The LACM(CIT) locs. 180 and 217 are present in Dry Canyon, which lies about 2 miles east of the Brea Canyon area. The stratigraphic positions of LACM(CIT) locs. 180 and 217 are very low in the middle member; however, it is difficult to trace individual beds from Dry Canyon to Brea Canyon. The stratigraphic positions of LACM(CIT) locs. 180 and 217 are within approximately 20 m of bed CS1 in Brea Canyon.

Figure 4 shows the stratigraphic relations of the vertebrate fossil localities and local faunas of Simi Valley. The stratigraphic ranges of the taxa within the Brea Canyon section and from the Dry Canyon localities are shown in Table 1. Descriptions and stratigraphic horizons of all the LACM(CIT) localities in Simi Valley, as well as the taxa these localities yielded during the present study, are presented in the Appendix.

## SYSTEMATIC PALEONTOLOGY

Golz and Lillegraven (1977) listed the majority of taxa from the Sespe Formation in Simi Valley. Included here are new taxa, new material representing poorly known taxa, and chronologic range extensions.

### Order Primates

### Infraorder Tarsiiformes
### Gregory, 1915

### Family Omomyidae
### Trouessart, 1879

### Subfamily sp. Omomyinae
### Trouessart, 1879

### Genus *Dyseolemur*
### Stock, 1934a

### *Dyseolemur pacificus*
### Stock, 1934a

Figure 5

*Dyseolemur pacificus* Stock, 1934a:954–959, pl. 1, figs. 1–3.

**MATERIAL.** LACM 128888, partial right dentary with partial $M_1$ and $M_2$.

**LOCALITY.** LACM(CIT) 128.

**AGE AND FAUNA.** Latest Uintan or earliest Duchesnean, Strathern Local Fauna.

**DISCUSSION.** The $M_1$ of LACM 128888 is badly damaged. The $M_2$, well preserved with only slight wear, has the diagnostic characters of *Dyseolemur,* including a metastylid and a short paracristid between the paraconid and protoconid. Dimensions of $M_2$ are A–P = 2.24, TRI–TR = 1.92, and TAL–TR = 1.95. The $M_2$ is morphologically indistinguishable from that of *D. pacificus* from the Brea Canyon Local Fauna.

*Dyseolemur pacificus* was previously known from the late Uintan Brea Canyon, Tapo Canyon, and Laguna Riviera Local Faunas (Golz and Lillegraven, 1977) and is also recorded in the latest Uintan or earliest Duchesnean Camp San Onofre Local Fauna (Lillegraven, 1980). The recovery of *D. pacificus* from LACM(CIT) loc. 128 represents the highest stratigraphic occurrence of this species in Simi Valley.

### Genus *Macrotarsius*
### Clark, 1941

### ***Macrotarsius roederi***
### **new species**

Figure 6; Table 2

**HOLOTYPE.** LACM 128928, partial right dentary with $I_2$ root, canine root, and $P_2$–$M_3$.

**TYPE LOCALITY.** LACM 5660.

**AGE AND FAUNA.** Late Uintan, Brea Canyon Local Fauna.

**ETYMOLOGY.** Named in honor of Mark A. Roeder, whose contributions to vertebrate paleontology include the recovery of large samples of Eocene fossil vertebrates from marine and nonmarine deposits in southern California over the last 20 years. Mr. Roeder discovered the type specimen of *M. roederi* while screen washing matrix from the Sespe Formation during an ongoing mitigation program at the Simi Valley Landfill.

**DIAGNOSIS.** Differs from *Macrotarsius jepseni* Robinson, 1968, in having the following characters: molars uncrowded, premolars and molars equally spaced, resulting in greater $P_3$–$M_3$ length; lack of distinct diastema between $P_2$ and $P_3$; $P_3$ paraconid smaller; $P_4$ larger, less reduced relative to molars, trigonid more well defined; $M_3$ smaller, narrower; accessory crests of metaconids and paraconids less complete; ramus deeper, more robust. Differs from *Macrotarsius siegerti* Robinson, 1968, and *Macrotarsius montanus* Clark, 1941, in having the following characters: premolars and molars much less crowded; $P_2$ much less reduced; $P_4$ less reduced relative to molars; lower molars smaller; accessory crests of metaconids and paraconids less developed. It further differs from *M. siegerti* in having larger $P_4$ and narrower $M_3$. It further differs from *M. montanus* in having longer and narrower $P_4$, and much smaller lower molars. Differs from *Ourayia uintensis* (Osborn, 1895), in having the following characters: $P_3$ not taller than $P_4$; $P_4$ trigonid more molariform; $P_4$ paraconid distinct and placed more anterolingually; molar cusps with accessory crests; metaconids prominent. Differs from *Hemiacodon gracilis* Marsh, 1872, in having the following characters: $P_2$ less reduced; $P_3$ not taller than $P_4$; premolars and molars less crowded; metaconids and paraconids with accessory crests; lower molars quadrate with less expanded talonids; cristae obliqua connected to posterior base of protoconids

Table 1. Stratigraphic ranges of Eocene mammalian taxa in Simi Valley. Systematic list modified from Golz and Lillegraven (1977), Savage and Russell (1983), Black and Sutton (1984), Mason (1988), and the results of the present study. Fossiliferous horizons included below each local fauna (LF) are in relative stratigraphic positions from lowest (CS1) to highest (SS22). Additional key references included in brackets. DCLOCS. refers to Dry Canyon localities LACM(CIT) 180 and 217.

| | Tapo Canyon LF | | Brea Canyon LF | | | | |
|---|---|---|---|---|---|---|---|
| Taxa | CS1 | DCLOCS. | CS2 | CS3 | SS4 | CS4 | CS5 |
| Marsupialia | | | | | | | |
| Didelphidae | | | | | | | |
| *Peratherium* sp., cf. *P. knighti* McGrew, 1959 [Lillegraven, 1976] | — | X | — | X | — | — | — |
| *Peradectes californicus* (Stock, 1936a) [Krishtalka and Stucky, 1983] | — | — | — | X | — | — | — |
| Pantolesta | | | | | | | |
| Pantolestoidea | | | | | | | |
| *Simidectes merriami* Stock, 1933b | — | — | — | — | — | — | — |
| Apatotheria | | | | | | | |
| Apatemyidae | | | | | | | |
| *Apatemys downsi* Gazin, 1958 [Walsh, 1987] | — | X | — | — | — | — | — |
| Creodonta | | | | | | | |
| Hyaenodontidae | | | | | | | |
| *Hyaenodon vetus* Stock, 1933a | — | — | — | — | — | — | — |
| *Hyaenodon venturae* Mellett, 1977 | — | — | — | — | — | — | — |
| Carnivora | | | | | | | |
| Miacidae | | | | | | | |
| *Procyonodictis progressus* (Stock, 1935b) [Mason, 1988] | — | X | X | — | — | — | — |
| *Miacis? hookwayi* Stock, 1934c | — | X | — | — | — | — | — |
| *Tapocyon occidentalis* Stock, 1934c | — | X | — | X | — | — | — |
| Insectivora | | | | | | | |
| Dormaaliidae | | | | | | | |
| *Sespedectes singularis* Stock, 1935c | X | X | X | X | — | X | — |
| *Proterixoides davisi* Stock, 1935c | — | X | X | X | — | X | — |
| Primates? | | | | | | | |
| Microsyopidae | | | | | | | |
| *Craseops sylvestris* Stock, 1934b | — | X | — | — | — | — | — |
| Primates | | | | | | | |
| Omomyidae | | | | | | | |
| *Phenacolemur* sp., cf. *P. shifrae* Robinson, 1968 [Mason, 1988] | — | X | — | — | — | — | — |
| *Dyseolemur pacificus* Stock, 1934a | — | X | X | X | — | — | — |
| *Chumashius balchi* Stock, 1933d | — | — | — | — | — | — | — |
| *Macrotarsius roederi* n. sp. [this paper] | — | — | — | X | — | — | — |
| Omomyid n. gen. and sp. [Mason, 1988] | — | X | — | — | — | — | — |
| Perissodactyla | | | | | | | |
| Brontotheriidae | | | | | | | |
| *Duchesneodus californicus* (Stock, 1935d) [Lucas and Schoch, 1982] | — | — | — | — | — | — | — |
| Helaletidae | | | | | | | |
| *Dilophodon* sp. [Stock, 1936c] | — | X | — | — | — | — | — |
| Hyracodontidae | | | | | | | |
| *Triplopus? woodi* Stock, 1936c | — | — | — | — | — | — | — |
| Amynodontidae | | | | | | | |
| *Amynodon* sp., cf. *A. advenus* Marsh, 1875 [Stock, 1939] | — | — | X | — | X | — | — |
| *Amynodontopsis bodei* Stock, 1933c | — | — | — | — | — | — | — |
| Artiodactyla | | | | | | | |
| Dichobunidae | | | | | | | |
| *Tapochoerus eggressus* (Stock, 1934b) | — | X | X | X | — | — | — |

Table 1. Extended.

| Strathern LF | | | Pearson Ranch LF | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CS8 | CS13 | CS14 | SS15 | CS15 | SS16 | CS16 | CS17 | SS18 | CS18 | CS20 | SS21 | SS22 |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | X | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | X | — | — |
| — | — | — | — | — | — | — | — | — | — | X | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | X | X | — | X | X | X | X | — | — | X | — | X |
| — | X | — | — | X | — | — | — | — | — | X | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | X | — | — | — | — | — | — | — | — | — | — |
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| — | — | — | X | — | — | X | — | X | — | X | — | X |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| X | X | — | — | — | — | X | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | X | X | — | X | — | X | X | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |

**Table 1. Continued.**

| Taxa | Tapo Canyon LF | | Brea Canyon LF | | | | |
|---|---|---|---|---|---|---|---|
| | CS1 | DCLOCS. | CS2 | CS3 | SS4 | CS4 | CS5 |
| Agriochoeridae | | | | | | | |
| *Protoreodon "pumilus"* [Golz, 1976; this paper] | — | X | X | X | — | X | — |
| *Protoreodon pacificus* Golz, 1976 | — | — | — | — | — | — | — |
| Protoceratidae | | | | | | | |
| *Leptoreodon edwardsi* Stock, 1936b | — | X | — | — | — | — | — |
| *Leptoreodon stocki* n. sp. [this paper] | X | — | X | X | X | X | X |
| *Leptoreodon pusillus* Golz, 1976 | — | — | — | — | — | — | X |
| *Leptoreodon* sp., cf. *L. pusillus* [this paper] | — | — | — | — | — | — | — |
| Oromerycidae | | | | | | | |
| *Protylopus* sp., cf. *P. petersoni* Wortman, 1898 [Golz, 1976] | — | — | — | X | — | — | — |
| *Protylopus pearsonensis* Golz, 1976 | — | — | — | — | — | — | — |
| *Protylopus stocki* Golz, 1976 | — | — | X | X | — | — | — |
| *Protylopus? robustus* Golz, 1976 | — | — | X | — | — | — | — |
| *Protylopus?* sp., aff. *P. robustus* Golz, 1976 | — | — | X | — | — | — | — |
| *Protylopus* sp., cf. *P.? robustus* Golz, 1976 [this paper] | — | — | — | — | X | — | — |
| *Eotylopus* sp. [Golz, 1976] | — | — | — | — | — | — | — |
| Hypertragulidae | | | | | | | |
| *Simimeryx hudsoni* Stock, 1934d | — | — | — | — | — | — | — |
| *Simimeryx* n. sp. [Mason, 1988] | — | X | — | — | — | — | — |
| Rodentia | | | | | | | |
| Ischyromyidae | | | | | | | |
| *Leptotomus* sp., cf. *L. caryophillus* Wilson, 1940a [Golz and Lillegraven, 1977] | — | X | — | — | — | — | — |
| *Leptotomus* sp., cf. *L. leptodus* (Cope, 1873) [Golz and Lillegraven, 1977] | — | X | — | — | — | — | — |
| *Tapomys tapensis* (Wilson, 1940a) | — | X | — | — | — | — | — |
| *Tapomys* sp. [Mason, 1988] | — | — | X | — | — | — | — |
| *Mytonomys burkei* (Wilson, 1940a) | — | — | X | X | X | — | — |
| *Mytonomys* sp., cf. *M. mytonensis* (Cope, 1873) [Mason, 1988; this paper] | — | — | — | — | — | — | — |
| *Microparamys* sp. D [Wood, 1962] | — | X | — | — | — | — | — |
| *Microparamys tricus* (Wilson, 1940a) | — | — | — | — | — | — | — |
| *Ischyrotomus* sp., cf. *I. compressidens* (Peterson, 1919) [Wood, 1962] | — | X | — | — | — | — | — |
| *Rapamys fricki* Wilson, 1940a | — | — | X | — | — | — | — |
| *Rapamys* sp. [Golz and Lillegraven, 1977] | — | — | — | X | — | — | — |
| *Rapamys* sp. indet. [this paper] | — | — | — | — | — | — | — |
| Ischyromyidae? | | | | | | | |
| *Eohaplomys tradux* Stock, 1935a | — | X | — | — | — | — | — |
| *Eohaplomys serus* Stock, 1935a | — | — | X | — | — | — | — |
| *Eohaplomys matutinus* Stock, 1935a | — | — | — | X | — | X | — |
| Cylindrodontidae | | | | | | | |
| *Pareumys* sp. [Wilson, 1940c] | X | — | — | X | — | — | — |
| *Pareumys* sp., near *P. milleri* Peterson, 1919 [Wilson, 1940c; this paper] | — | — | X | — | — | — | — |
| *Presbymys lophatus* Wilson, 1949 | — | — | — | — | — | — | — |
| Family ?Geomyidae | | | | | | | |
| *Griphomys alecer* Wilson, 1940b | — | — | X | X | — | — | — |
| Family ?Zapodidae | | | | | | | |
| *Simimys simplex* (Wilson, 1935a) [Wilson, 1935b] | — | X | X | X | — | — | — |

Table 1. Extended, Continued.

| Strathern LF | | | Pearson Ranch LF | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CS8 | CS13 | CS14 | SS15 | CS15 | SS16 | CS16 | CS17 | SS18 | CS18 | CS20 | SS21 | SS22 |
| X | X | — | — | — | — | — | — | — | — | — | — | — |
| — | X | — | X | X | — | X | — | X | — | X | X | X |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | X | X | — | — | X | X | — | — | — | X | — | X |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | X | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | X | — | — | — | X | — | — | X | — | X | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | X | — | — |
| X | X | — | X | X | X | X | X | X | X | X | X | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
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| — | — | — | — | — | — | — | — | — | — | — | — | — |
| X | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | X | — | X | — | — | — | X | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | X | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | X | — | — | — | X | — | — |
| — | — | — | — | — | — | — | — | — | — | X | — | — |
| — | — | — | — | — | — | — | — | X | — | X | — | — |
| — | — | — | — | — | — | X | — | — | — | X | — | — |

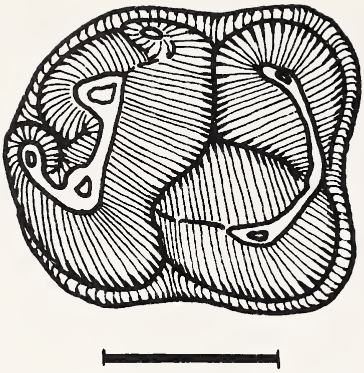

Figure 5. *Dyseolemur pacificus* Stock, $RM_2$, LACM 128888; occlusal view. Scale = 1 mm.

and positioned more labially; $M_{1-2}$ lacking hypoconulids; horizontal ramus straighter.

**DESCRIPTION.** *Macrotarsius roederi* is known only from the holotype. The $I_2$ is represented by the root, which is unpaired and anteroposteriorly compressed at the base; however, the shape of the alveolus suggests the tooth was more circular at the alevolar border. The tooth appears to have been smaller than the canine.

The canine is also represented by the root. The tooth is single rooted and the base of the crown is slightly compressed anteroposteriorly resulting in an oval cross section. The size of the root indicates that the canine was larger than $I_2$ and $P_2$.

The premolars form a continuous series, with $P_2$ smaller than $P_3$, and $P_3$ smaller than $P_4$. They are

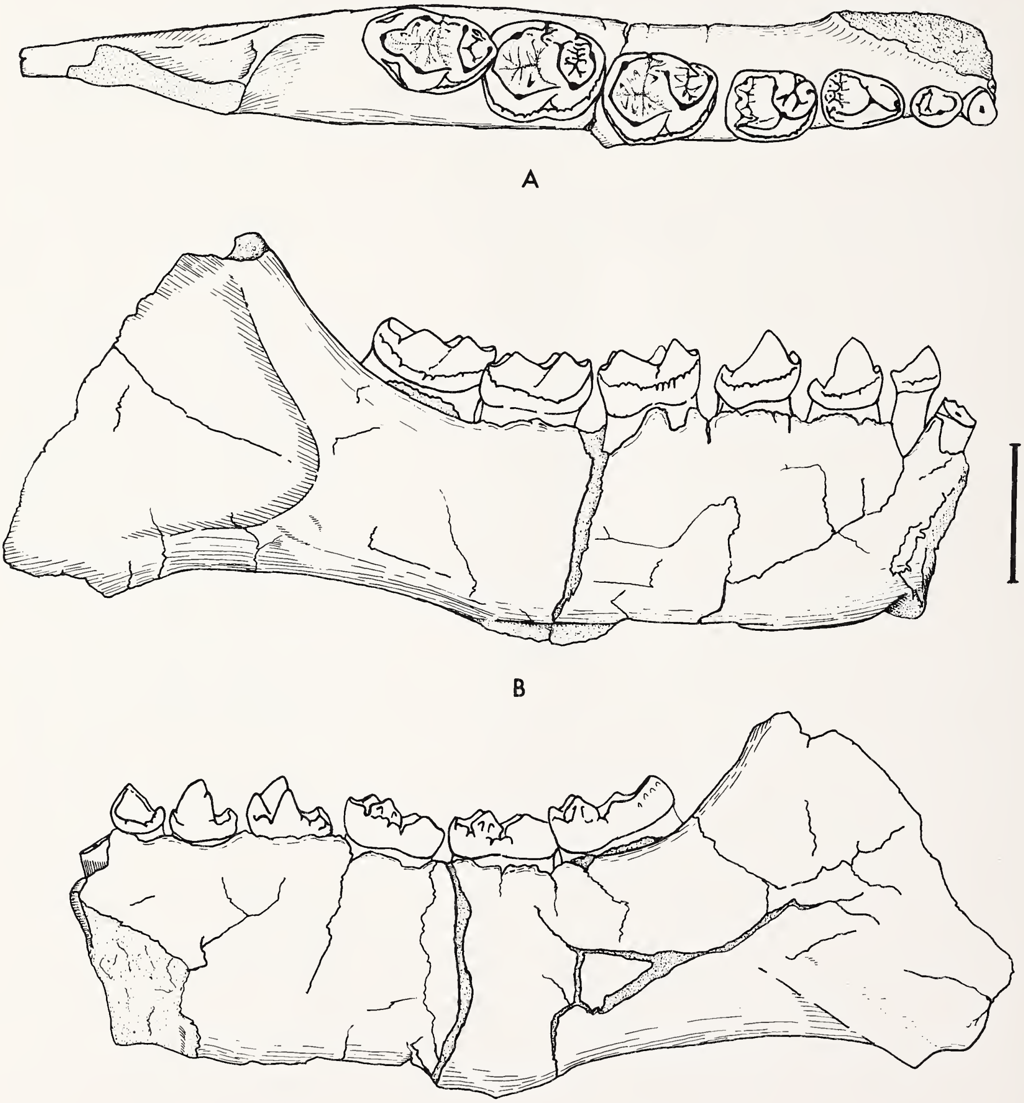

Figure 6. *Macrotarsius roederi* n. sp., holotype, partial right dentary with $I_2$ root, partial canine, and $P_2$–$M_3$, LACM 128928. **A.** Occlusal view. **B.** Lingual view. **C.** Labial view. Scale = 5 mm.

equally spaced and uncrowded. The enamel of the premolars becomes increasingly crenulated from $P_2$ (little crenulation) to $P_4$ (moderate crenulation).

The $P_2$ is single-rooted, slightly elongated anteroposteriorly, and expanded posteriorly. It is reduced in size relative to $P_3$ and $P_4$. The tooth lacks a paraconid and metaconid. A crista obliqua originates from the apex of the protoconid and terminates at a small distinct cusp at the posterolabial corner of the tooth. The posterior cingulum is slightly expanded, giving the tooth the general appearance of $P_3$ and $P_4$. The anterior, lingual, and posterior cingulae are prominent and continuous. The labial cingulum is moderately distinct.

The $P_3$ is two-rooted, elongated anteroposteriorly, and expanded posteriorly. A very small paraconid is present on the anterior cingulum. A slight bulge on the labial aspect of the protoconid suggests an incipient metaconid. The crista obliqua originates at the apex of the protoconid and terminates at a distinct cusp just lingual to the posterolabial corner of the tooth. The posterior cingulum is expanded and has several distinct cusps. The anterior, labial, and posterior cingulae are prominent and continuous. The $P_3$ is smaller but equal in height to $P_4$.

The $P_4$ is two-rooted and subquadrate in shape. The well-developed paraconid and metaconid form a distinct trigonid. The paraconid is positioned towards the lingual aspect of the tooth and is connected to the protoconid by a paralophid that is gently curved. The metaconid is connected to the protoconid by a protolophid that is almost straight, short, and notched apically. The cusps of the trigonid are unequal in height, with the paraconid the lowest, the protoconid the highest, and the metaconid intermediate. A small cusp is present at the anterolabial corner of the tooth between the paraconid and metaconid. The anterior, labial, and posterior cingulae are prominent and continuous. The crista obliqua originates at the apex of the protoconid and terminates at the posterior cingulum, near a small distinct cusp. This cusp, the largest of three present along the posterior cingulum, possesses a very small crest that is connected to the base of the posterior aspect of the protoconid.

The lower molars are characterized by a subquadrate to quadrate shape, metaconids and protoconids with accessory crests (cutting edges of Szalay and Delson, 1979), highly crenulated enamel, V-shaped trigonids, and expanded talonids.

The $M_1$ is subquadrate in shape. The trigonid is V-shaped with a low, gently curved paralophid with little apical relief and a relatively straight protolophid that is notched at the center. The paraconid is lower than the metaconid and protoconid, and a small accessory crest extends posteriorly from the paraconid towards the metaconid. The well-developed paraconid is positioned lingually. The metaconid is well developed, does not connect with the entoconid, and possesses two small accessory crests, one extending anteriorly towards the paraconid and one extending posteriorly towards the entoconid. The crista obliqua is located labially where it originates at the base of the posterior aspect of the protoconid. The hypoconulid is not represented by a true cusp, and the position it would normally occupy is reduced to a notch in the postcristid. The talonid is expanded transversely. The anterior, labial, and posterior cingulae are prominent and continuous.

**Table 2. Measurements (in mm) of teeth in holotype (LACM 128928) of *Macrotarsius roederi* n. sp. from the Brea Canyon Local Fauna.**

| Dimension | | Measurement |
|---|---|---|
| $P_2$ | A–P | 1.85 |
| | TR | 1.55 |
| $P_3$ | A–P | 2.68 |
| | TR | 2.78 |
| $P_4$ | A–P | 3.43 |
| | TR | 2.96 |
| $M_1$ | A–P | 4.06 |
| | TRI–TR | 3.05 |
| | TAL–TR | 3.36 |
| $M_2$ | A–P | 4.17 |
| | TRI–TR | 3.24 |
| | TAL–TR | 3.35 |
| $M_3$ | A–P | 4.76 |
| | TRI–TR | 2.88 |
| | TAL–TR | 2.91 |

The $M_2$ is very similar to $M_1$, but it is more quadrate in shape because the trigonid is slightly more expanded, resulting in a longer protolophid. The paraconid is well developed and positioned lingually.

The $M_3$ is similar to $M_1$ and $M_2$, except that it possesses a robust hypoconulid.

**DISCUSSION.** *Macrotarsius* Clark, 1941, *Ourayia* Gazin, 1958, and *Mytonius* Robinson, 1968, represent a group of related omomyine primate genera whose taxonomy has been the subject of controversy (see Gazin, 1958; Simons, 1961; Robinson, 1968; Szalay, 1976; Krishtalka, 1978; Szalay and Delson, 1979). At times *Hemiacodon* Marsh, 1872, has also been included in this group; however, more recent revisions indicate it is not closely related to the other taxa (Krishtalka, 1978; Szalay, 1976). Szalay (1976) and Szalay and Delson (1979) do not recognize *Mytonius hopsoni* Robinson, 1968, or *Macrotarsius jepseni* Robinson, 1968, as valid taxa, but instead refer them to *Ourayia uintensis* (Osborn, 1895). Krishtalka (1978), however, considers *O. uintensis*, *M. hopsoni*, and *M. jepseni* as generically and specifically distinct taxa. Krishtalka (1978) provides convincing evidence that *M. hopsoni* is a valid taxon and that *M. jepseni* is not referable to *O. uintensis*. The comprehensive systematic revision presented by Krishtalka (1978) is followed here.

The presence of *Macrotarsius* along the Pacific Coast during the Eocene was first suggested by Lillegraven (1980) on the basis of three isolated lower molars recovered from the lower Uintan Friars and Mission Valley Formations in the San Diego area. The specimens were identified as ?*Macrotarsius* sp., near *M. jepseni;* however, the diagnostic lower premolars are unknown, and comparison with *Macrotarsius roederi* is difficult. It is not likely that these molars represent *M. roederi* because the M$_3$ in the San Diego sample is considerably smaller than the M$_3$ in *M. roederi.* Moreover, Mason (1988) identified the other two molars from the San Diego area as *Ourayia* instead of *Macrotarsius.*

Mason (1988, unpublished) described a new genus and species of omomyine primate from LACM(CIT) loc. 180 (Tapo Canyon Local Fauna). *Macrotarsius roederi* differs from this new taxon in having the following characters: teeth smaller; M$_{1-3}$ metaconids not twinned; M$_3$ much less reduced relative to M$_{1-2}$; M$_3$ hypoconulid positioned more labially.

*Macrotarsius roederi* is the most primitive member of the genus. *Macrotarsius siegerti* and *M. montanus* are more derived in their greater development of the accessory crests of the metaconids and paraconids and much greater reduction of the premolars relative to the molars. Based on similarities in the lower teeth, *M. roederi* appears to be most closely related to *M. jepseni;* however, *M. jepseni* is also more derived in having the following characters: premolars reduced relative to molars; P$_3$–M$_3$ crowded; P$_{2-3}$ diastema present.

## Order Artiodactyla

## Family Oromerycidae
## Gazin, 1955

### Genus *Protylopus* Wortman, 1898

### *Protylopus*? sp.,
### cf. *P.*? *robustus*
### Golz, 1976

Figure 7

**MATERIAL.** LACM 128910, partial right dentary with M$_3$.

**LOCALITY.** LACM 5627.

**AGE AND FAUNA.** Late Uintan, Brea Canyon Local Fauna.

**DISCUSSION.** The M$_3$ of LACM 128910 is similar to those of *Protylopus*? *robustus* but is larger (A–P = 17.8, TR = 9.0), is more robust, and has more complete labial and lingual cingulae. Additional material may demonstrate that the specimen is assignable to *P.*? *robustus;* however, at this time its distinctive characters warrant separation from *P*? *robustus.* Golz (1976) referred two specimens (LACM 26365, 26366) from LACM(CIT) loc. 207 to *Protylopus*? sp., aff. *P.*? *robustus.* The M$_3$ of LACM 128910 is much larger than those of *P.*? sp., aff. *P.*? *robustus.*

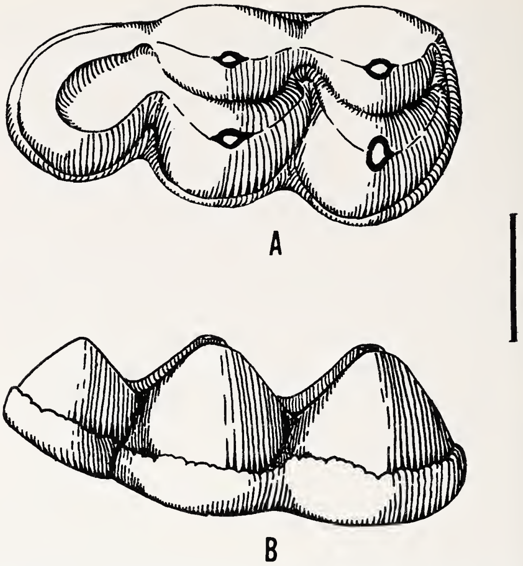

**Figure 7.** *Protylopus*? sp., cf. *P.*? *robustus* Golz, RM$_3$, LACM 128910. **A.** Occlusal view. **B.** Labial view. Scale = 5 mm.

## Family Protoceratidae
## Marsh, 1891

## Subfamily Leptotragulinae
## Zittel, 1893

### Genus *Leptoreodon*
### Wortman, 1898

### *Leptoreodon pusillus*
### Golz, 1976

Figure 8; Table 3

*Leptoredon pusillus* Golz, 1976:62–65, figs. 36–38.

**MATERIAL.** LACM 128904, RM$_2$, LM$_3$.

**LOCALITY.** LACM 5620.

**AGE AND FAUNA.** Late Uintan, Brea Canyon Local Fauna.

**DISCUSSION.** The two lower molars of *Leptoreodon* from Simi Valley are intermediate in size between *L. pusillus* Golz, 1976, and *L. edwardsi* Stock, 1936a; however, morphologically, they appear to be very similar to those of *L. pusillus.* The lingual indentations between the metaconids and entoconids of the lower molars are slightly deeper than those in *L. edwardsi,* but are similar in depth to those in *L. pusillus.* The postfossettid of M$_3$ is open to the hypoconulid fossettid. The lingual ends of the posterior crests of the hypoconids are not lobate, as in *L. edwardsi,* but are less developed, as in *L. pusillus.* The Brea Canyon molars differ from those in the holotype of *L. pusillus* in having slightly more robust anterior and posterior cingulae, and from all other species of *Leptoreodon* (*L. edwardsi; L. leptolophus* Golz, 1976; *L. major* Golz, 1976; *L. marshi* Wortman, 1898; *L. stocki* n. sp.) by their smaller size.

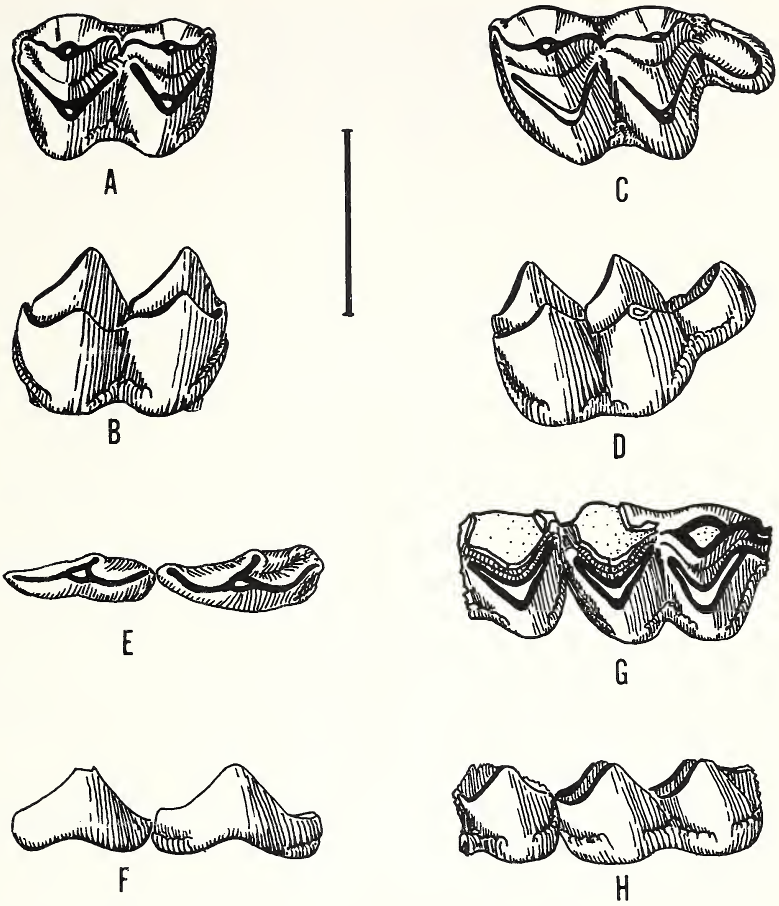

**Figure 8.** *Leptoreodon pusillus* Golz (A–D), and *L.* sp., cf. *L. pusillus* (E–H). *Leptoreodon pusillus,* $RM_2$, LACM 128904. **A.** Occlusal view. **B.** Labial view; $LM_3$, LACM 128904. **C.** Occlusal view. **D.** Labial view. *Leptoreodon* sp., cf. *L. pusillus,* $RP_{3-4}$, LACM 42401. **E.** Occlusal view. **F.** Labial view; partial $M_{2-3}$, LACM 42401. **G.** Occlusal view. **H.** Labial view. Scale = 5 mm.

The size range of the lower molars in *L. pusillus* is unknown because only the holotype (UCR 14005) from the Laguna Riviera Local Fauna in California (Golz, 1976), and three lower molar fragments from Texas (Wilson, 1986) were previously assigned to the species. The lower molars of *L. pusillus* from Brea Canyon are only slightly larger than those in the holotype (Table 3).

The presence of *L. pusillus* in the Brea Canyon and Laguna Riviera Local Faunas, and the Whistler Squat and Serendipity Local Faunas of Texas (Wilson, 1986), suggests this species was widespread in the southern United States during the middle Eocene.

### *Leptoreodon* sp., cf. *L. pusillus* Golz, 1976

Figure 8

**MATERIAL.** LACM 42401, partial left dentary with $P_{3-4}$, partial $M_2$ and $M_3$.

**LOCALITY.** LACM(CIT) 128.

**AGE AND FAUNA.** Latest Uintan or earliest Duchesnean, Strathern Local Fauna.

**DISCUSSION.** D.J. Golz, during his curatorship of the CIT Sespe Formation collection at the LACM, made a notation on the back of the specimen label for LACM 42401 questioning the recovery of this specimen from LACM(CIT) loc. 128; however, the

**Table 3. Measurements (in mm) of teeth of *Leptoreodon pusillus* Golz (1976) from the Brea Canyon Local Fauna and holotype (UCR 14005) from the Laguna Riviera Local Fauna.**

| | LACM 128904 | | |
|---|---|---|---|
| Dimension | Right | Left | UCR 14005 |
| $M_2$ A–P | 6.0 | | 5.3 |
| TR | 4.4 | | 4.1 |
| $M_3$ A–P | | 8.9 | 8.2 |
| TR | | 4.4 | 4.8 |

original CIT label suggests that it was associated with other specimens that were definitely collected at LACM(CIT) loc. 128.

The premolars of LACM 42401 are very similar in size and morphology to those in the holotype of *L. pusillus* (UCR 14005). Dimensions of the teeth in the holotype are A–P = 4.6, TR = 1.8 for $P_3$, and A–P = 4.9, TR = 2.5 for $P_4$; those for the Brea Canyon specimen are A–P = 4.8, TR = 1.95 for $P_3$, and A–P = 4.9, TR = 2.8 for $P_4$. The only notable difference between the holotype of *L. pusillus* and the Brea Canyon specimen is the development of a small swelling on the posterolabial crest of $P_3$ in the Brea Canyon specimen, suggesting an incipient metaconid. However, this difference may not be taxonomically significant because Golz (1976) reported the presence or absence of a metaconid on $P_3$ is variable in large samples of *L. edwardsi.*

The hypoconid on the $P_4$ of the Brea Canyon specimen is weakly developed, as in *L. pusillus,* and differs from *L. edwardsi, L. leptolophus,* and *L. stocki* n. sp., in which a well-developed hypoconid is present. The entoconid is weakly developed, as in *L. pusillus.* The metaconid is prominent, as in *L. pusillus* and *L. edwardsi,* but not elliptical, as in *L. leptolophus* and *L. stocki.* A distinct paraconid is present and closely associated with the protolophid, as in *L. pusillus,* but differs from *L. edwardsi,* in which the paraconid is larger and more widely separated from the protolophid. The Brea Canyon premolars differ from those of all other species of *Leptoreodon* (*L. edwardsi, L. leptolophus, L. major, L. marshi, L. stocki* n. sp.) by their smaller size.

The partial lower molars from Simi Valley cannot be distinguished from those in the holotype of *L. pusillus.* The postfossettid of $M_3$ is open to the hypoconulid fossettid, and a worn accessory cuspulid, which appears to be similar to the simple accessory cuspulid in *L. pusillus,* is present.

The specimen from LACM(CIT) loc. 128 is assigned to *Leptoreodon* sp., cf. *L. pusillus,* because of the presence of the small metaconid on $P_3$; however, additional material may demonstrate that the presence of this character varies intraspecifically, as in *L. edwardsi* (Golz, 1976), and the Brea Canyon specimen could then be assigned to *L. pusillus.*

## *Leptoreodon stocki*
## new species

Figures 9, 10; Tables 4–7

*Leptoreodon* sp., aff. *L. leptolophus* Golz, 1976:71–73, figs. 44, 45.

**HOLOTYPE:** LACM 26368, partial left dentary with $P_4$–$M_3$.

**TYPE LOCALITY.** LACM(CIT) 202.

**HYPODIGM.** LACM 26367, partial left maxilla with partial $P^4$ and $M^{1-3}$; LACM 128907, partial left maxilla with C, $P^3$–$M^3$, partial left dentary with $P_1$–$M_3$, and partial right dentary with $P_1$–$M_3$; LACM 27389, $RP^4$; LACM 52206, $LP^4$; LACM 128908, $RM^{2-3}$; LACM 128890, $RM^3$; LACM 128889, $LM^3$; LACM 128903, $RM^1$; LACM 128909, partial left dentary with $P_{2-4}$; LACM 27390, partial right dentary with $P_{2-4}$; LACM 27391, partial left dentary with $M_3$; LACM(CIT) 1948, partial left dentary with $P_3$–$M_3$; LACM 27392, partial right dentary with $P_4$–$M_3$; LACM 27393, partial right dentary with partial $M_2$ and $M_3$; LACM 27394, partial left dentary with $P_4$–$M_3$; LACM 128912, $RP_4$; LACM 27395, partial right dentary with partial $P_{2-3}$, $P_4$, and $M_2$; LACM 27396, partial right dentary with $M_3$; LACM 128896, partial left dentary with $M_{1-2}$; LACM 128913, partial right dentary with $M_{1-3}$; LACM 128891, $LM_1$; LACM(CIT) 477, partial left dentary with $M_{1-2}$ and partial $M_3$; LACM 42403, partial $LM_1$; LACM 52207, partial left dentary with $M_1$; LACM 52208, partial right dentary with partial $M_2$ and $M_3$; LACM 42402, partial $RM_3$; LACM 128911, partial left dentary with partial $M_3$.

**AGES, FAUNAS, AND DISTRIBUTION.** Late Uintan, Tapo Canyon Local Fauna: LACM loc. 5621. Late Uintan, Brea Canyon Local Fauna: LACM(CIT) locs. 127, 151, 202, 207; LACM locs. 5618, 5625, 5628, 5631. Latest Uintan or earliest Duchesnean, Strathern Local Fauna: LACM(CIT) loc. 128. Early Duchesnean, Pearson Ranch Local Fauna: LACM(CIT) loc. 146; LACM locs. 5611, 5646, 5648.

**ETYMOLOGY.** Named in honor of the late Chester Stock. Stock, while at the CIT, was the first researcher to conduct extensive vertebrate paleontologic investigations in the Simi Valley area and the first to recognize the presence of Eocene land mammal assemblages in the Sespe Formation.

**DIAGNOSIS.** Larger than *L. pusillus, L. edwardsi,* and *L. leptolophus;* about equal in size to *L. marshi;* smaller than *L. major.* Differs from *L. pusillus, L. edwardsi, L. major,* and *L. marshi* in having the following characters: teeth with slightly stronger and more slender crests; molar mesostyles and metastyles more sharply flexed; $P_4$ paraconid and metaconid less bulbous; molar parastylids more sharply flexed; $M_3$ hypoconulid relatively more slender and anteroposteriorly elongated; accessory cuspulid of the $M_3$ hypoconulid moderately to well developed, posterolingually directed, and crescent-shaped. Differs from *L. leptolophus* in having the following characters: teeth 5 to 19 percent larger; $P^3$ anterolabial cingulum more prominent, labial indentation deeper, metastyle and parastyle more prominent, and incipient protocone more posteriorly positioned; $P^4$ metastyle and parastyle slightly more prominent and labial indentation more prominent; upper molar cingulae more prominent with greater development of double anterior cingulae; $P_4$ wider, less reduced relative to $M_1$, and paraconid and metaconid slightly more robust; molars relatively wider and more robust cingulae.

**DESCRIPTION.** A single canine tooth (LACM 128907) is known. This tooth is relatively robust and roughly triangular in cross section. The anterior

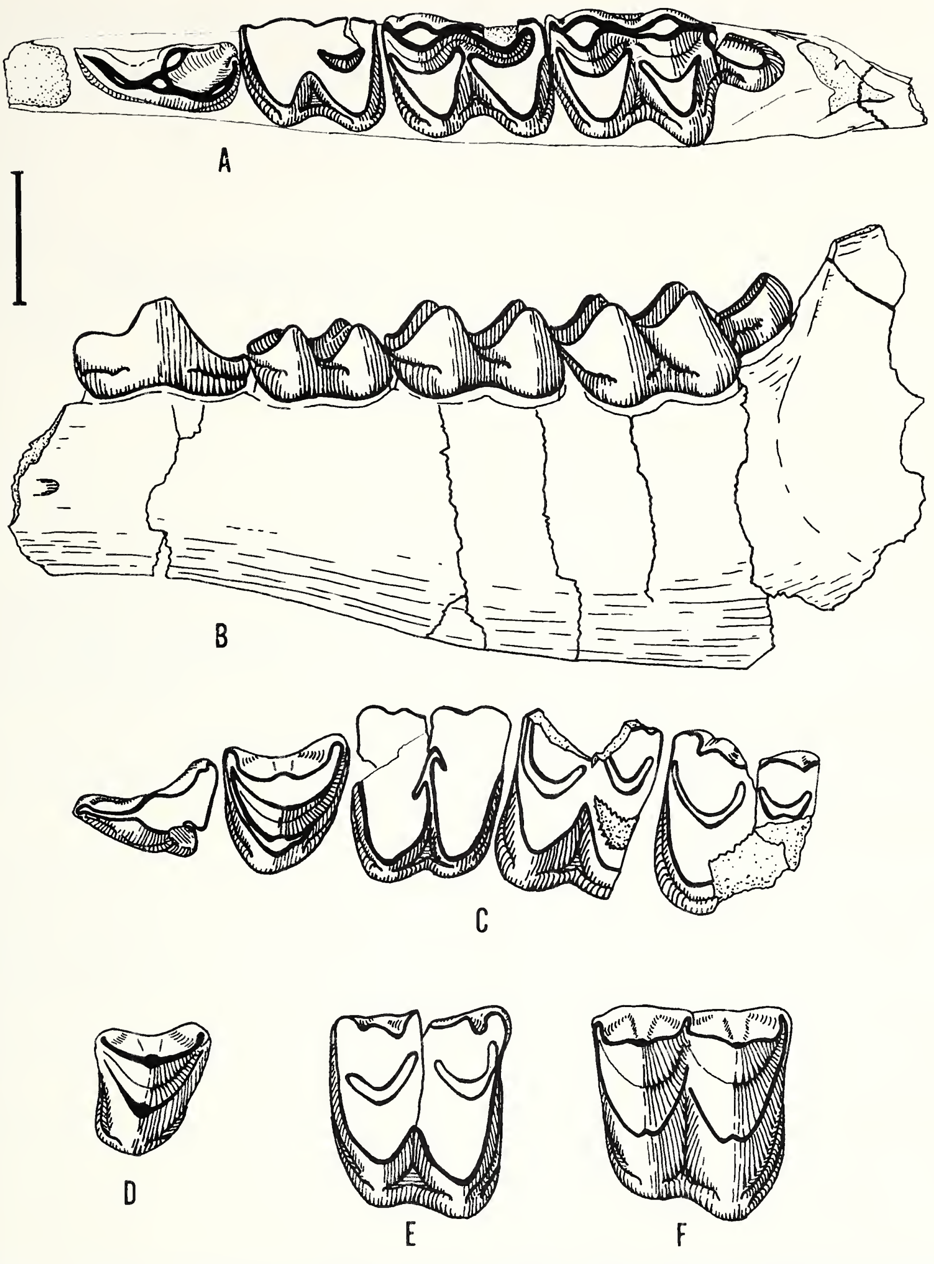

**Figure 9.** *Leptoreodon stocki* n. sp., holotype, partial left dentary with $P_4$–$M_3$, LACM 26368. **A.** Occlusal view. **B.** Labial view; $LP^3$–$M^3$, LACM 128907. **C.** Occlusal view; $LP^4$, LACM 52206. **D.** Occlusal view; $RM^3$, LACM 128908. **E.** Occlusal view; $RM^3$, LACM 128890. **F.** Occlusal view. Scale = 5 mm.

apex is rounded and the posterior margin relatively flat. The enamel extends much farther on the labial surface than on the lingual surface. A well-developed rib is present on the lingual surface, and a moderately deep groove on the labial surface.

The $P^3$ is represented by one moderately worn specimen, LACM 128907. The tooth is three-rooted and elongated anteroposteriorly and has a distinct labial bulge suggestive of an incipient protocone. The paracone is centered somewhat lingually, resulting in a central indentation of the labial wall of the tooth. Moderately curved crests extend from the paracone to the metastyle and parastyle. The anterolingual cingulum is very prominent, and the posterior cingulum is moderately prominent.

The $P^4$ is triangular in occlusal outline and somewhat transversely expanded. The mestastyle and parastyle are well developed, and the crests that extend from the paracone to the parastyle and metastyle are sharply curved. The protocone is cres-

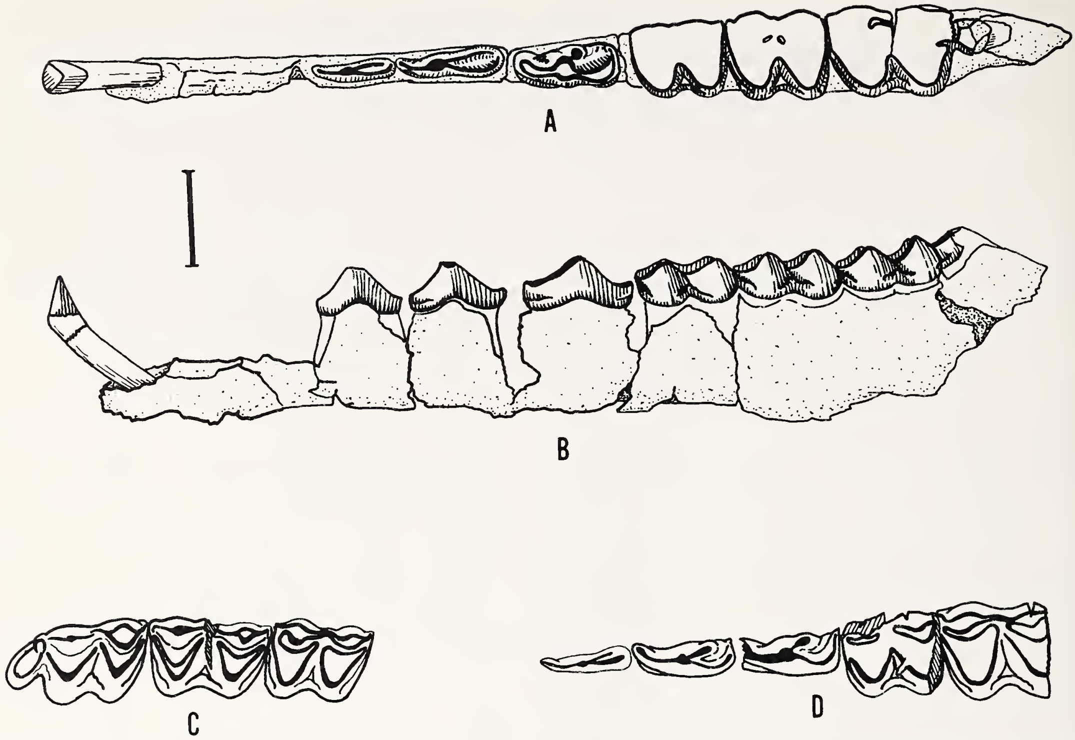

**Figure 10.** *Leptoreodon stocki* n. sp., $LP_1$–$M_3$, LACM 128907. **A.** Occlusal view. **B.** Labial view; $RM_{1-3}$, LACM 128913. **C.** Occlusal view; $LP_2$–partial $M_2$, LACM 128905. **D.** Occlusal view. Scale = 5 mm.

centic and the posterior crest of the protocone extends toward, but does not connect with, the posterolingual margin of the metastyle. The anterior and posterior cingulae are moderately prominent.

The upper molars have sharply compressed styles and slender crests. The lingual cingulum is moderately prominent and in some specimens (LACM 128907, 128908) is continuous across the base of the protocone and metaconule. The anterior cingulum is well developed, and in some specimens a double anterior cingulum is present (Fig. 9F).

The $P_1$ is caniniform and represented by three specimens showing well-worn, anteriorly directed facets. A diastema approximately 8 mm long is present between $P_1$ and $P_2$.

The $P_2$ is a simple, elongated, single-cusped tooth. The anterolabial and posterolabial crests are gently

**Table 4. Measurements (in mm) of upper teeth of *Leptoreodon stocki* n. sp. from Simi Valley. (N = sample size; OR = observed range; $\bar{X}$ = mean; SD = standard deviation; CV = coefficient of variation.)**

| Dimension | | N | OR | $\bar{X}$ | SD | CV |
|---|---|---|---|---|---|---|
| C | A–P | 1 | 4.2 | — | — | — |
| | TR | 1 | 3.8 | — | — | — |
| $P^3$ | A–P | 1 | 7.2 | — | — | — |
| | TR | 1 | 4.6 | — | — | — |
| $P^4$ | A–P | 3 | 5.2–5.8 | 5.7 | 0.29 | 4.7 |
| | TR | 3 | 6.0–6.2 | 6.15 | 0.20 | 3.4 |
| $M^1$ | A–P | 2 | 7.0–7.1 | 7.05 | 0.07 | 1.0 |
| | TR | 3 | 8.2–9.1 | 8.8 | 0.49 | 5.6 |
| $M^2$ | A–P | 2 | 7.5–7.9 | 7.7 | 0.28 | 3.6 |
| | TR | 2 | 9.9 | — | — | — |
| $M^3$ | A–P | 4 | 8.2–8.4 | 8.3 | 0.09 | 1.1 |
| | TR | 4 | 10.0–10.8 | 10.5 | 0.35 | 3.4 |

**Table 5. Measurements (in mm) of lower teeth of *Leptoreodon stocki* n. sp. from Simi Valley. See Table 4 for key to abbreviations.**

| Dimension | | N | OR | $\bar{X}$ | SD | CV |
|---|---|---|---|---|---|---|
| $P_1$ | A–P | 2 | 4.3–4.4 | 4.35 | 0.07 | 1.6 |
| | TR | 2 | 2.6–2.8 | 2.7 | 0.14 | 5.2 |
| $P_2$ | A–P | 5 | 5.3–6.0 | 5.7 | 0.25 | 4.4 |
| | TR | 3 | 2.0–2.2 | 2.1 | 0.14 | 6.6 |
| $P_3$ | A–P | 5 | 5.7–6.8 | 6.3 | 0.37 | 5.9 |
| | TR | 3 | 3.0–3.2 | 3.1 | 0.13 | 4.3 |
| $P_4$ | A–P | 9 | 6.1–7.2 | 6.7 | 0.36 | 5.4 |
| | TR | 10 | 3.2–4.3 | 3.7 | 0.33 | 9.0 |
| $M_1$ | A–P | 12 | 6.0–7.2 | 6.6 | 0.40 | 6.0 |
| | TR | 12 | 4.7–5.8 | 5.2 | 0.35 | 6.7 |
| $M_2$ | A–P | 11 | 7.3–8.7 | 7.8 | 0.49 | 6.2 |
| | TR | 13 | 5.6–6.3 | 6.0 | 0.26 | 4.4 |
| $M_3$ | A–P | 10 | 10.8–11.8 | 11.3 | 0.40 | 3.5 |
| | TR | 14 | 5.4–6.5 | 6.0 | 0.35 | 5.8 |

**Table 6. Measurements (in mm) of upper teeth for specimens of *Leptoreodon stocki* n. sp. from Simi Valley.**

| Specimen number (LACM) | Dimension | | | | | |
|---|---|---|---|---|---|---|
| | *C* A-P:TR | $P^3$ A-P:TR | $P^4$ A-P:TR | $M^1$ A-P:TR | $M^2$ A-P:TR | $M^3$ A-P:TR |
| 128907 | 4.2:3.8 | 7.2:4.6 | 5.8:6.2 | —:8.2 | —:9.4a* | —:— |
| 128908 | | | | | 7.5:9.9 | 8.2:10.4 |
| 128890 | | | | | | 8.4:10.8 |
| 128889 | | | | | | 8.4:10.7 |
| 128903 | | | | 7.0:9.1 | | |
| 27389 | | | 5.7:6.4 | | | |
| 52206 | | | 5.3:6.0 | | | |
| 26367 | | | | 7.1:8.8 | 7.9:9.9 | 8.4:10.0 |

* a = approximate.

curved lingually. The posterolingual crest is moderately developed.

The $P_3$ is elongated and slightly wider than $P_2$. The anterolabial and posterolabial crests are gently curved lingually. The paraconid is developed as a small distinct lingual bulge. The posterolingual crest is well developed, and the posterior basin may be open or closed posteriorly. The metaconid is slightly developed as a bulge on the posterolingual crest.

The $P_4$ is wider than $P_2$ and $P_3$ and slightly narrower than $M_1$. The anterolabial crest is gently curved lingually. A paraconid is present as a conical or oval bulge on the anterolabial crest. The hypoconid is weakly developed as a small bulge on the posterolabial crest. An incipient entoconid is present and ranges in shape from a very small bulge to a slightly larger conical bulge. The metaconid is generally a small conical bulge connected by a small crest to the posterolingual crest; however, in one specimen (LACM 128912), the metaconid is only a small swelling on the posterolingual crest. The anterolingual and posterior cingulae are variable, ranging from very weakly to moderately well developed.

The $M_{1-3}$ labial cusps are strongly crescentic and relatively flat in occlusal outline. The parastylids

**Table 7. Measurements (in mm) of lower teeth for specimens of *Leptoreodon stocki* n. sp. from Brea Canyon area.**

| Specimen number (LACM) | Dimension | | | | | | |
|---|---|---|---|---|---|---|---|
| | $P_1$ A-P:TR | $P_2$ A-P:TR | $P_3$ A-P:TR | $P_4$ A-P:TR | $M_1$ A-P:TR | $M_2$ A-P:TR | $M_3$ A-P:TR |
| 27389 | | | | 6.8:3.8 | 6.4:5.4 | 8.0:6.2 | |
| 27390 | | 6.0:— | 6.3a:— | | | | |
| 27395 | | 5.3:— | 5.7:— | 6.9:3.5a* | | | |
| 26368 | | | | 7.4:4.0 | 6.8:5.5 | 8.2:6.1a | 11.7a:6.5 |
| 27392 | | | | 6.3a:3.3 | 6.5:5.1 | 7.5:5.7 | 11.6a:5.8 |
| 27394 | | | | 6.1:3.2 | 6.1:4.9 | 7.6:6.0 | —:5.8 |
| 27393 | | | | | | —:6.3 | 11.3:5.8 |
| 27391 | | | | | | | 11.0:5.9 |
| 27396 | | | | | | | 11.8:6.5 |
| 42403 | | | | | 7.2:— | | |
| 52207 | | | | | 6.8:5.4 | | |
| 52208 | | | | | | —:5.9 | 11.8:6.5 |
| 42402 | | | | | | | —:6.3a |
| (CIT) 477 | | | | | 6.8:5.0 | 8.2:6.2 | —:6.3a |
| 128905 | | 5.6:2.3 | 6.5:2.9 | —:3.7 | —:— | —:— | |
| 128907 | 4.4:2.6 | 5.7:2.2 | 6.4:3.0 | 6.7:3.9 | 6.5:5.8 | 7.3:6.2 | 11.3:6.1 |
| 128907 | 4.3:2.9 | 5.7:2.0 | 6.8:3.0 | 7.2:3.8 | 6.3:5.6 | 7.5:5.7 | 11.2a:6.0 |
| 128896 | | | | | 7.2:5.1 | 8.5:5.9 | |
| 128909 | | 5.7:2.2 | 6.3:3.2 | —:4.3 | | | |
| 128912 | | | | 6.5:3.8 | | | |
| 128911 | | | | | | | —:5.8 |
| 128891 | | | | | 7.2:5.1 | | |
| 128913 | | | | | 6.0:4.7 | 7.4:5.6 | 10.8:5.5 |

* a = approximate.

are small but distinct and sharply flexed. The termini of the posterior crest of the metaconid and the anterior crest of entoconid are separate and slightly overlap each other in unworn teeth; however, these crests connect with wear. The posterior crest of the entoconid is well developed and connected to the posterior crest of the hypoconid. A small cuspulid is present between the protoconid and hypoconid on the lingual cingulum in unworm specimens. This cuspulid disappears with wear. The anterior and posterior cingulae are very prominent. The hypoconulid of $M_3$ is long and narrow and is usually closed off lingually from the postfossettid by a crescent-shaped accessory cuspulid. This cuspulid varies in shape from a partial crescent to an almost complete circle.

**DISCUSSION.** Golz (1976) assigned specimens from LACM(CIT) locs. 202 and 207 (Brea Canyon Local Fauna) to *Leptoreodon* sp., aff. *L. leptolophus*, recognizing these specimens as different from those of the closely related *L. leptolophus* from the Laguna Riviera Local Fauna. With the discovery of additional material from Simi Valley, it is now possible to compare this sample with *L. leptolophus*.

Golz (1976) considered the distinct crescent-shaped accessory cuspulid of the $M_3$ hypoconulid the most important character demonstrating *L. leptlophus* and the Simi Valley sample of *Leptoreodon* were related. This cuspulid closes off the postfossettid from the hypoconulid fossettid in all specimens of *L. leptolophus*. Golz (1976) noted that a specimen (LACM 27391) from LACM(CIT) loc. 207 in Simi Valley exhibited only partial closure of the $M_3$ hypoconulid fossettid, whereas a specimen (LACM 27393) from higher in the section at LACM(CIT) loc. 202 approaches the more closed condition of the fossettid, as in *L. leptolophus*. Another specimen (LACM 27396) from LACM(CIT) loc. 202 has a broken accessory cuspulid, although the lingual wall shows complete closure of the fossettid. A series of relatively unworn $M_3$'s is now available that spans the stratigraphic interval from the level of LACM(CIT) loc. 207 (upper Uintan) to that of LACM loc. 5648 (Duchesnean). Golz (1976) suggested the degree of closure of the $M_3$ hypoconulid fossettid increased with decreasing geologic age, and this suggestion is supported by the new material discovered during the present study. The accessory cuspulid in earlier specimens [from the level of LACM(CIT) loc. 207] develops posteriorly as a partial crescent extending from the entostylid, in later samples [from the levels of LACM(CIT) locs. 127 and 202] extends labially as a complete crescent closing off the postfossettid from the hypoconulid fossettid, and in the latest sample (from the level of LACM loc. 5648) forms an almost complete circle. The variation seen in the accessory cuspulid suggests a morphocline extending from a more primitive (open hypoconulid, less complex accessory cuspulid) to a more derived state (closed hypoconulid, complex accessory cuspulid) through time.

The development of double anterior cingulae on the $M^{1-3}$ may also represent a morphocline. The $M^{2-3}$ (LACM 128908) from the level of LACM(CIT) loc. 151 (upper Uintan) exhibits moderately developed double anterior cingulae, whereas $M^3$'s (LACM 128889, 128890) from LACM(CIT) loc. 128 (uppermost Uintan or lowest Duchesnean) exhibit well-developed double anterior cingulae. Although the sample of *L. stocki* upper molars is small, it appears that the presence of a double anterior cingulum is an advanced character, which reaches its greatest development in specimens from higher stratigraphic levels.

All specimens referred to *L. leptolophus* by Golz (1976) are from one locality (UCR loc. RV-6830 = UCMP loc. V-6839, LACM loc. 68102) and represent a single population. The following alternative interpretations of the observed variation in *Leptoreodon* arose during the present study: 1) the specimens from Simi Valley are a single species representing a temporal morphocline; or 2) more than one species exists; 3) the Simi Valley samples belong to *L. leptolophus*, which exhibits a wide range of intraspecific variation; or 4) the Simi Valley samples represent a distinct species. The morphologic characters that Golz (1976) used to separate the Simi Valley specimens from *L. leptolophus* and additional diagnostic characters based on the new material seem to corroborate his recognition of the Simi Valley samples as a distinct species.

To test the assumption that the Simi Valley samples represent a distinct species, a series of statistical analyses were performed to measure the degree of variability in the Simi Valley samples of *L. stocki* and to compare the Simi Valley samples with the topotypic sample of *L. leptolophus*. In addition, the specimens from Texas identified as *L. leptolophus* by Wilson (1984) were compared with the topotypic sample of *L. leptolophus* to help clarify the extent of geographic variation between these samples of *Leptoreodon*. The samples were first divided into three groups: group 1 represented all late Uintan specimens from Simi Valley; group 2 represented all Duchesnean specimens from Simi Valley; and group 3 represented the topotypic specimens of *L. leptolophus* from the Laguna Riviera Local Fauna.

The coefficient of variation (CV) is a good measure of relative dispersion within a population, and most species exhibit CV's of about five or six for linear measurements (Simpson *et al.*, 1960). Table 8 presents the CV's calculated for each group and various combinations of the groups. In addition, the CV's calculated by Golz (1976) for *L. edwardsi*, a well-defined species of *Leptoreodon*, were included to allow comparison of these CV's with those of the Simi Valley samples of *L. stocki*. In Table 9, a summary of the distribution of CV's greater than seven for each grouping in Table 8 indicates groups 1 and 1+2 exhibit a comparatively low degree of dispersion that is consistent with that for a single species; however, when grouped with

Table 8. Coefficients of variation (CV) for groups of samples of *Leptoreodon* (group 1 = Uintan specimens of *L. stocki* n. sp. from Simi Valley; group 2 = Duchesnean specimens of *L. stocki* from Simi Valley; group 3 = *L. leptolophus* Golz (1976) from Laguna Riviera Local Fauna). CV's calculated by Golz (1976) for large sample of *L. edwardsi* from Dry Canyon are included for comparison. See Table 4 for key to abbreviations.

| | | Group | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | | 1+2 | | 3 | | 1+3 | | 1+2+3 | | *L. edwardsi* | |
| Dimension | | N | CV | N | CV | N | CV | N | CV | N | CV | N | CV |
| $P^4$ | A-P | 3 | 4.7 | 3 | 4.7* | 6 | 2.7 | 9 | 6.0 | 9 | 6.0 | 10 | 8.1 |
| | TR | 3 | 3.4 | 3 | 3.4* | 6 | 4.5 | 9 | 4.1 | 9 | 4.1 | 10 | 4.7 |
| $M^1$ | A-P | 2 | 1.0 | 2 | 1.0* | 13 | 4.8 | 15 | 5.8 | 15 | 5.8 | 10 | 3.6 |
| | TR | 3 | 5.6 | 3 | 5.6* | 12 | 2.6 | 15 | 7.7 | 15 | 7.7 | 10 | 4.3 |
| $M^2$ | A-P | 2 | 3.6 | 2 | 3.6* | 15 | 3.4 | 17 | 4.4 | 17 | 4.4 | 10 | 6.3 |
| | TR | 2 | 0 | 2 | 0* | 15 | 3.8 | 17 | 6.3 | 17 | 6.3 | 10 | 5.6 |
| $M^3$ | A-P | 2 | 1.7 | 4 | 0.1 | 12 | 5.3 | 14 | 7.7 | 16 | 7.7 | 10 | 4.3 |
| | TR | 2 | 0 | 4 | 3.4 | 12 | 5.9 | 14 | 8.1 | 16 | 10.1 | 10 | 4.3 |
| $P_3$ | A-P | 5 | 4.4 | 5 | 5.9* | 5 | 2.1 | 10 | 4.7 | 10 | 4.7 | 10 | 3.2 |
| | TR | 3 | 6.6 | 3 | 4.3* | 5 | 16.2 | 8 | 18.6 | 8 | 18.6 | 10 | 8.5 |
| $P_4$ | A-P | 9 | 5.4 | 9 | 5.4* | 4 | 2.7 | 13 | 5.8 | 13 | 5.8 | 20 | 4.4 |
| | TR | 10 | 9.0 | 10 | 9.0* | 4 | 0.05 | 14 | 9.7 | 14 | 9.7 | 20 | 5.0 |
| $M_1$ | A-P | 7 | 3.9 | 12 | 6.0 | 14 | 4.1 | 21 | 3.9 | 26 | 5.3 | 20 | 4.4 |
| | TR | 7 | 5.6 | 12 | 6.7 | 14 | 12.0 | 21 | 12.8 | 26 | 11.7 | 20 | 6.2 |
| $M_2$ | A-P | 7 | 6.3 | 11 | 6.2 | 10 | 4.8 | 17 | 6.3 | 21 | 7.0 | 20 | 3.8 |
| | TR | 9 | 3.9 | 13 | 4.4 | 10 | 9.6 | 21 | 11.1 | 24 | 10.5 | 20 | 4.7 |
| $M_3$ | A-P | 8 | 2.4 | 10 | 3.5 | 5 | 2.7 | 13 | 4.1 | 15 | 4.1 | 20 | 2.5 |
| | TR | 12 | 4.8 | 14 | 5.8 | 5 | 13.2 | 14 | 11.5 | 19 | 10.7 | 20 | 5.5 |

* Indicates no Duchesnean specimens were present in sample.

the sample of *L. leptolophus* from the Laguna Riviera Local Fauna, a high degree of variation is apparent and suggests a degree of heterogeneity sufficient to recognize the Simi Valley samples as a distinct species.

To further test the degree of heterogeneity between *L. leptolophus* and the Simi Valley samples of *L. stocki*, Student's t-tests were performed using the linear dimensions of $M_1$ and $M_2$. These teeth were selected because they are relatively evenly distributed between groups and represent the largest number of measurable specimens. The null hypothesis was that the Laguna Riviera sample (group 3) and the Simi Valley samples (groups 1 and 1+2) were not significantly different and represent the same species. The calculations resulted in rejection of the null hypothesis and indicate a significant difference exists between the Simi Valley and the Laguna Riviera samples (Table 10). To further test if *L. leptolophus* and *L. stocki* represent distinct species, Student's t-tests comparing a single specimen to a sample were performed. The holotype of *L. leptolophus* (UCR 13499) was compared with the Simi Valley groups 1 and 1+2. Conversely, the holotype of *L. stocki* (LACM 26368) was compared with the Laguna Riviera sample (group 3). The null hypothesis was that the holotypes do not differ statistically from the other species sample. The calculations led to rejection of the null hypothesis and indicate that each holotype is significantly different from the other species sample (Table 11). To determine the probability that either combination of groups represents the normal distribution expected for a single species, a Goodness-of-Fit test was performed using the width of $M_1$ for groups 1+2 and 1+2+3 (Table 12). The null hypothesis that groups 1+2 (late Uintan and Duchesnean, Simi Valley) represent a single species was accepted. The null hypothesis that groups 1+2+3 represent a single species was rejected. In summary, all the statistical tests performed support recognition of *L. stocki* as a species distinct from *L. leptolophus*.

Only a few Duchesnean specimens of *L. stocki* are known. To determine if these specimens and

Table 9. Summary of coefficients of variation (CV) greater than seven for groups of samples of *Leptoreodon* presented in Table 8. See Table 4 for key to abbreviations.

| | Group | | | | | |
|---|---|---|---|---|---|---|
| CV | 1 | 1+2 | 3 | 1+3 | 1+2+3 | *L. edwardsi* |
| >10 | 0 | 0 | 3 | 4 | 5 | 0 |
| >9 | 0 | 0 | 4 | 5 | 6 | 0 |
| >8 | 1 | 1 | 4 | 6 | 6 | 2 |
| >7 | 1 | 1 | 4 | 7 | 8 | 2 |

**Table 10.** Results of Student's t-tests comparing sample of *Leptoreodon stocki* n. sp. (group 1 = Uintan specimens; group 1+2 = Uintan and Duchesnean specimens) from Simi Valley and sample of *L. leptolophus* (group 3) from Laguna Riviera Local Fauna. Null hypothesis is that samples of *L. stocki* and *L. leptolophus* do not differ significantly and represent same species. (D.F. = degrees of freedom; t = t-value calculated; P = probability.)

| Samples compared | Dimension | | D.F. | t | P | Null hyp. |
|---|---|---|---|---|---|---|
| 1 and 3 | $M_1$ | A–P | 23 | 1.398 | 0.172 | accepted |
| | | TR | 18 | 3.831 | 0.002 | rejected |
| | $M_2$ | A–P | 15 | 2.390 | 0.029 | rejected |
| | | TR | 19 | 6.184 | <0.001 | rejected |
| (1+2) and 3 | $M_1$ | A–P | 20 | 1.254 | 0.222 | accepted |
| | | TR | 22 | 3.486 | 0.002 | rejected |
| | $M_2$ | A–P | 19 | 2.689 | 0.014 | rejected |
| | | TR | 22 | 6.107 | <0.001 | rejected |

the late Uintan specimens belong to the same species, a series of Student's t-tests comparing a single specimen and a sample were performed. The null hypothesis was that each Duchesnean specimen [LACM(CIT) 477, LACM 128891, 128896, 128913] does not differ significantly from the late Uintan sample (group 1). The calculations resulted in acceptance of the null hypothesis, indicating the Duchesnean and Uintan samples from Simi Valley represent one species (Table 13). However, as seen in Table 13, one Duchesnean specimen (LACM 128913) exhibits relatively low probabilities (P) of belonging to *L. stocki;* nevertheless, all measurements met the 95% or greater level of confidence, and, thus, this specimen probably represents a small individual of *L. stocki.* It must be noted that the temporal range of *L. stocki* may be greater than one million years and it should not be unexpected to find a moderate degree of variability in this species through time.

**Table 11.** Results of Student's t-tests comparing single specimen and known sample. Holotype of *Leptoreodon leptolophus* (UCR 13499) compared with samples of *L. stocki* n. sp. from Simi Valley (group 1 = Uintan specimens; group 1+2 = Uintan and Duchesnean specimens) and holotype of *L. stocki* n. sp. (LACM 26368), compared with sample of *L. leptolophus* from Laguna Riviera Local Fauna (group 3). Null hypothesis is that each holotype does not differ significantly from other species sample. See Table 10 for key to abbreviations.

| Samples compared | Dimension | | D.F. | t | P | Null hyp. |
|---|---|---|---|---|---|---|
| UCR 13499 and 1 | $M_1$ | A–P | 6 | 1.230 | 0.26 | accepted |
| | | TR | 6 | 1.237 | 0.26 | accepted |
| | $M_2$ | A–P | 6 | 1.321 | 0.23 | accepted |
| | | TR | 8 | 3.632 | 0.01 | rejected |
| | $M_3$ | A–P | 7 | 1.670 | 0.14 | accepted |
| | | TR | 8 | 2.938 | 0.02 | rejected |
| UCR 13499 and 1+2 | $M_1$ | A–P | 11 | 0.625 | >0.50 | accepted |
| | | TR | 11 | 0.42 | >0.70 | accepted |
| | $M_2$ | A–P | 10 | 1.815 | 0.10 | accepted |
| | | TR | 12 | 2.857 | 0.01 | rejected |
| | $M_3$ | A–P | 9 | 0.953 | >0.30 | accepted |
| | | TR | 13 | 2.208 | 0.04 | rejected |
| LACM 26368 and 3 | $M_1$ | A–P | 13 | 2.452 | 0.03 | rejected |
| | | TR | 13 | 0.778 | >0.40 | accepted |
| | $M_2$ | A–P | 9 | 2.418 | 0.04 | rejected |
| | | TR | 9 | 2.825 | 0.02 | rejected |
| | $M_3$ | A–P | 4 | 3.126 | 0.04 | rejected |
| | | TR | 4 | 2.044 | 0.11 | accepted |

A series of Student's t-tests was performed to determine if the specimens from the Candelaria Local Fauna of Texas (TMM 40276-17, 40187-1) referred to *L. leptolophus* by Wilson (1984) represent members of the same species as does the topotypic sample. The calculations resulted in acceptance of the null hypothesis that the Texas specimens are representatives of *L. leptolophus* (Table 14) and confirm Wilson's (1984) premise that *L. leptolophus* was widespread in the southern United States during the middle Eocene.

In summary, *L. stocki* represents a distinct species of *Leptoreodon* that is present in the upper Uintan to lower Duchesnean of Simi Valley and is closely related to *L. leptolophus* of the Laguna Riviera Local Fauna.

**Table 12.** Results of Goodness-of-Fit tests on transverse width of $M_1$. Two groups were analyzed: 1+2 includes Uintan and Duchesnean specimens of *Leptoreodon stocki* n. sp. from Simi Valley; 1+2+3 includes Uintan and Duchesnean specimens of *L. stocki* from Simi Valley and specimens of *L. leptolophus* from Laguna Riviera Local Fauna. Null hypothesis is that samples do not differ significantly and each group represents a single species. See Table 10 for abbreviations.

| Group | D.F. | Chi-square value | P | Null hyp. |
|---|---|---|---|---|
| 1+2 | 3 | 2.073 | 0.5574 | accepted |
| 1+2+3 | 3 | 20.28 | <0.005 | rejected |

**Table 13. Results of Student's t-tests comparing single specimen to known sample. Each Duchesnean specimen of *Leptoreodon stocki* [LACM 128896, 128891, 128913, LACM(CIT) 477] compared with Uintan sample of *L. stocki* (group 1). Null hypothesis is that each Duchesnean specimen does not differ significantly from Uintan sample and represents same species. See Table 10 for key to abbreviations.**

| Samples compared | Dimension | D.F. | t | P | Null hyp. |
|---|---|---|---|---|---|
| LACM 128896 and 1 | $M_1$ A–P | 6 | 2.062 | 0.08 | accepted |
| | TR | 6 | 0.928 | >0.60 | accepted |
| | $M_2$ A–P | 6 | 1.227 | 0.28 | accepted |
| | TR | 8 | 0.404 | >0.70 | accepted |
| LACM 128891 and 1 | $M_1$ A–P | 6 | 2.062 | 0.07 | accepted |
| | TR | 6 | 0.928 | >0.60 | accepted |
| LACM 128913 and 1 | $M_1$ A–P | 6 | 1.663 | 0.09 | accepted |
| | TR | 6 | 2.165 | 0.07 | accepted |
| | $M_2$ A–P | 6 | 0.755 | >0.40 | accepted |
| | TR | 8 | 1.614 | 0.14 | accepted |
| | $M_3$ A–P | 7 | 2.039 | 0.08 | accepted |
| | TR | 8 | 1.632 | 0.14 | accepted |
| LACM(CIT) 477 and 1 | $M_1$ A–P | 6 | 0.898 | 0.40 | accepted |
| | TR | 6 | 1.237 | 0.26 | accepted |
| | $M_2$ A–P | 6 | 0.661 | >0.40 | accepted |
| | TR | 8 | 0.807 | >0.40 | accepted |
| | $M_3$ A–P | — | — | — | — |
| | TR | 8 | 0.653 | >0.40 | accepted |

## Order Rodentia

### Family Ischyromyidae Alston, 1876

### Genus *Rapamys* Wilson, 1940a

### *Rapamys* sp. indet.

Figure 11

**MATERIAL.** LACM 128929, worn RM$_2$?.

**LOCALITY.** LACM 5645.

**AGE AND FAUNA.** Early Duchesnean, Pearson Ranch Local Fauna.

**DISCUSSION.** The lower molar is so worn that only generic assignment to *Rapamys* can be made. *Rapamys* has not been recorded previously in the Duchesnean of Simi Valley, although *Rapamys fricki* Wilson, 1940a, and *Rapamys* sp. A (Wood, 1962) have been recorded from lower in the Brea Canyon section at LACM(CIT) locs. 202 and 207. *Rapamys* sp. indet. is slightly larger than *Rapamys* sp. A and *R. fricki.*

### Subfamily Ailuravinae Michaux, 1968

### Genus *Mytonomys* Wood, 1956

### *Mytonomys burkei* (Wilson, 1940a)

Figure 12; Table 15

*Leptotomus burkei* Wilson, 1940a:73–74, pl. 2, figs. 1, 1a.

**Table 14. Results of Student's t-tests comparing single specimen and known sample. Specimens of *Leptoreodon leptolophus* from Texas (TMM 40276-17, 40187-1) compared with known sample of *L. leptolophus* (group 3) from Laguna Riviera Local Fauna. Null hypothesis is that each specimen from Texas does not differ significantly from known sample and represents the same species. See Table 10 for key abbreviations.**

| Samples compared | Dimension | D.F. | t | P | Null hyp. |
|---|---|---|---|---|---|
| TMM 40276-17 and 3 | $M_1$ A–P | 13 | 0.372 | >0.70 | accepted |
| | TR | 13 | 1.073 | 0.30 | accepted |
| | $M_2$ A–P | 9 | 0.545 | 0.40 | accepted |
| | TR | 9 | 1.751 | 0.11 | accepted |
| TMM 40187-1 and 3 | $M_1$ A–P | 13 | 1.486 | 0.16 | accepted |
| | TR | 13 | 1.252 | 0.23 | accepted |
| | $M_2$ A–P | 9 | 0 | >0.99 | accepted |
| | TR | 9 | 0 | >0.99 | accepted |

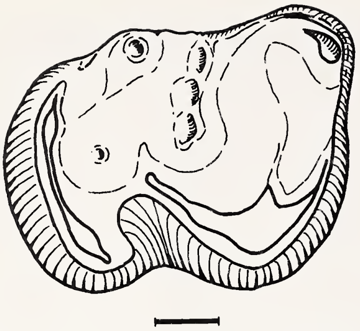

**Figure 11.** *Rapamys* sp. indet., worn LM$_3$?, LACM 128929; occlusal view. Scale = 1 mm.

*Mytonomys burkei* (Wilson): Wood, 1956:753.
*Leptotomus* sp., near *L. burkei* Wilson, 1940a, in part: Wood, 1962:229–231, fig. 84G, H.
*Mytonomys burkei* (Wilson): Korth, 1984:47; Korth, 1988:290.

**MATERIAL.** LACM 128931, partial lower incisor, LM$^2$?, LM$_2$?, and RM$_2$?; LACM 128930, partial right dentary with incisor root and P$_4$–M$_1$.

**LOCALITIES.** LACM 5625, 5626.

**AGE AND FAUNA.** Late Uintan, Brea Canyon Local Fauna.

**DESCRIPTION.** In cross section, the lower incisor of LACM 128931 is widened anteriorly, with a gently curved anterior face and a slightly flattened medial surface. The posterior portion of the tooth narrows to an irregular elongated crescent. The pulp cavity is an elongated oval. The anterior enamel band extends posteriorly well onto the lateral surface of the tooth, whereas it barely extends onto the medial surface. A very slight indication of grooving of the enamel is present, but the grooving does not result in any indentation of the enamel in cross section.

The well worn M$^2$? of LACM 128931 is very similar to an upper molar [LACM(CIT) 2178] tentatively referred to *Mytonomys burkei* by Wood (1962). A deep notch is present between the protocone and hypocone, accentuating the hypocone. The protocone is prominent, expanded labially, and a moderate notch is present anterior to the protocone. The anterior cingulum, although worn, is well developed and terminates at the labial margin of the parastyle. The mesostyle is large and appar-

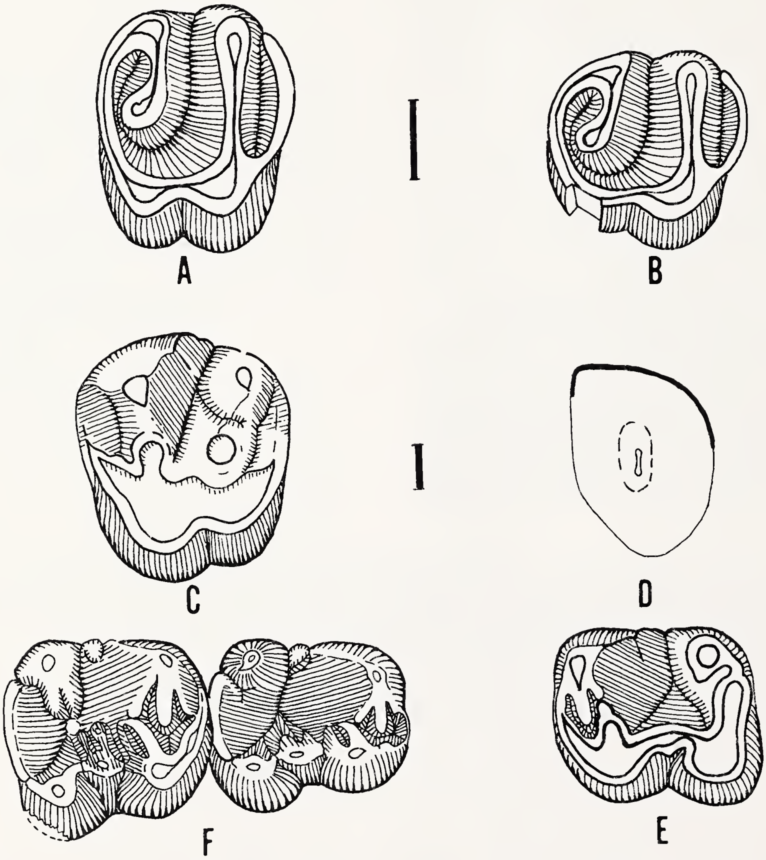

**Figure 12.** *Pareumys* sp., aff. *P. milleri* Peterson (A, B) and *Mytonomys burkei* Wilson (C–F). *Pareumys* sp., aff. *P. milleri*, RM$^2$, LACM 128892. **A.** Occlusal view; RM$^1$, LACM 128892. **B.** Occlusal view. Upper scale for A and B = 1 mm. *Mytonomys burkei*, LM$^2$?, LACM 128931. **C.** Occlusal view; RI$_1$, LACM 128931. **D.** Cross section; LM$_2$?, LACM 128931. **E.** Occlusal view; RP$_4$–M$_1$, LACM 128930. **F.** Occlusal view. Lower scale for C–E = 1 mm.

ently lacks an accessory loph directed towards the metaconule. The protoconule and metaconule are distinct, the latter being much larger. The curvature of the labial cusps is moderately convex. The enamel in the valleys was probably moderately crenulated because a small area just anterior to the protoconule, though very worn, still shows evidence of crenulation.

The slightly worn $P_4$ of LACM 128930 is unreduced and longer than the associated $M_1$. A well-developed accessory ridge extends from the metaconid into the trigonid between the anterolophid and metalophid. The metalophid (= protolophid of Wood, 1962) is almost complete and nearly closes off the trigonid posteriorly. The metaconid and protoconid are not widely separated, resulting in a relatively short metalophid. A distinct mesostylid and mesoconid are present. An entoconid crest is not present. The posterolophid is prominent, and a small cleft is present between the posterolophid and entoconid. The entoconid is elevated well above the posterolophid. The enamel is moderately crenuated.

The lower molars of LACM 128931, even in their worn state, have the accessory ridge of the metaconid and a remnant of the entoconid crest. The slightly worn $M_1$ of LACM 128930 is very similar in morphology to the specimens of *M. burkei* described by Wood (1962), except the entoconid and mesoconid crests are slightly less prominent. The posterolophid of LACM 128930 is prominent, and a small cleft is present between the posterolophid and entoconid.

**DISCUSSION.** *Mytonomys burkei* was originally described as *Leptotomus burkei* by Wilson (1940a). Wood (1956) proposed *Mytonomys*, typified by *M. robustus* (Peterson, 1919), and assigned specimens of *L. burkei* to the genus. Wood (1962) described material assigned to *M. burkei* and referred specimens originally identified as *Leptotomus* sp., near *L. burkei* by Wilson (1940a), to the species. Wood (1956, 1962) referred *Mytonomys* to the subfamily Prosciurinae, based on a number of diagnostic characters. Black (1968) discussed each character and refuted this assignment, concluding that *Mytonomys* is an ischyromyid, with no close relationship to the prosciurines. Wood (1976) tentatively included *Mytonomys* in the Ailuravinae, and Korth (1988) provided further evidence *Mytonomys* belongs in this subfamily. Korth (1984, 1988) reevaluated *Mytonomys* and referred *Pseudotomus coloradensis* (Wood, 1962) and *Leptotomus mytonensis* (Wood, 1962) to the genus, and synonymized *Leptotomus kayi* (Burke, 1934) with *M. robustus* (Peterson, 1919).

Only six specimens from the Sespe Formation have previously been referred to *Mytonomys burkei*, three from LACM(CIT) loc. 202 and three from LACM(CIT) loc. 207 (Wilson, 1940a; Wood, 1956, 1962; Mason, 1988). All of this material is fragmentary. Previously, the lower incisor was unknown and only an isolated upper molar [LACM(CIT) 2178] was referred to this species with uncertainty. This upper molar was illustrated by Wilson (1940a, pl. 2) and briefly described by Wood (1962). With the discovery of an upper molar [LACM(CIT) 128931] associated with lower teeth definitely referable to *M. burkei*, LACM(CIT) 2178 can now be confidently assigned to the species. Wood (1962) only cursorily described the previously known specimens of $P_4$ [LACM(CIT) 2174, 2176] of *M. burkei* because they are badly worn.

**Table 15. Measurements (in mm) of the teeth of *Mytonomys burkei* from Simi Valley.**

| Dimension | | LACM 128931 Right | LACM 128931 Left | LACM 128930 |
|---|---|---|---|---|
| $M^2$? | A–P | 5.96 | | |
| | TR | 4.91 | | |
| $\bar{I}$ | A–P | | 5.15 | |
| | TR | | 3.85 | |
| $P_4$ | A–P | | | 5.55 |
| | ANT–TR | | | 4.42 |
| | POST–TR | | | 5.45 |
| $M_1$ | A–P | | | 5.45 |
| | ANT–TR | | | 4.86 |
| | POST–TR | | | 5.15a* |
| $M_2$ | A–P | 5.19 | 5.20 | |
| | ANT–TR | 4.50 | 4.55 | |
| | POST–TR | — | 4.94 | |

* a = approximate.

The specimens (LACM 128930, 128931) described herein can be confidently referred to *Mytonomys* because the lower molars possess the diagnostic accessory ridge that extends from the metaconid into the trigonid between the anterolophid and metalophid (Wilson, 1940a; Wood, 1962; Black, 1968). These specimens are indistinguishable from those of *M. burkei* described by Wilson (1940a) and Wood (1962), except for the entoconid and mesoconid crests of the $M_1$ in LACM(CIT) 128930, which are not as prominent. Black (1968) found the development of the entoconid crest in *Mytonomys robustus* to be variable. The differences are minor and herein regarded as intraspecific variation.

The new specimens of *M. burkei* from the Sespe Formation described herein provide the following additional characters that distinguish *M. burkei* from *M. robustus:* mesostyle of upper molars lacking accessory loph directed toward metaconule; slightly less anterior notching of protocone; labial curvature of upper molar cusps slightly less convex; $P_4$ metaconid and protoconid not as widely separated; $P_4$ entoconid crest absent. These specimens also provide the following additional characters that distinguish *M. burkei* from *M. mytonensis:* larger; parastylar area of upper molar more expanded; $P_4$ larger than $M_1$; accessory lophs of lower cheek teeth better developed.

## Family Cylindrodontidae
## Miller and Gidley, 1918

### Genus *Pareumys*
### Peterson, 1919

### *Pareumys* sp.,
### aff. *P. milleri*
### Peterson, 1919

Figure 12

*Pareumys* sp., near *P. milleri* Peterson. Wilson, 1940c:99–101, pl. 1, figs. 1, 2, 6; pl. 2, fig. 1, 1a.
*Pareumys* sp., in part, Wilson, 1940c:102–103, pl. 1, fig. 3.

**MATERIAL.** LACM 128892, RM$^{1-2}$.

**LOCALITY.** LACM 3549.

**AGE AND FAUNA.** Late Uintan to early Duchesnean, Brea Canyon and Pearson Ranch Local Faunas.

**DESCRIPTION.** The M$^{1-2}$ of LACM 128892 have similarly structured lophs and are almost flat-topped [lophs about same height, except the anterior cingulum (= anteroloph), which is lower]. The protoloph is continuous from the protocone to the paracone. The metaloph bends posteriorly toward the posterior cingulum (= ectoloph), its base uniting with the cingulum and forming a small cleft on the occlusal surface between the protocone and cingulum. The posterior cingulum is prominent and continuous from the hypocone to metacone. A well-developed groove is present on the M$^1$ between the protocone and hypocone and accentuates a large distinct hypocone. A similar, but less prominent, groove is present on the M$^2$ between the protocone and hypocone. A portion of the posterolabial wall of the M$^2$ hypocone is missing; however, this cusp apparently was moderately distinct. The dimensions of LACM 128892 are A–P = 1.77, anterior TR = 1.92 for M$^1$, and A–P = 2.09, anterior TR = 2.42, posterior TR = 2.35 for M$^2$.

**DISCUSSION.** Specimens of *Pareumys* sp., aff. *P. milleri*, are very rare in the Sespe Formation; only two upper molars [LACM(CIT) 2214, 2215] have previously been referred to this species (Wilson, 1940c). Fusion of the metalophs with the posterior cingulae of the upper molars in LACM 128892 is not as complete as in LACM(CIT) 2214 and 2215; however, this may be due to differences in stage of wear. S.L. Walsh (personal communication) considers the fusion of the metaloph with posterior cingulum in the larger samples of *Pareumys* from the Friars and Mission Valley Formations in the San Diego area to be variable and not a reliable diagnostic character.

According to Wilson (1940c) the sample of *Pareumys* from the Pearson Ranch Local Fauna differs from *P. milleri* in having the following characters: P$_4$ slightly more reduced; metalophid apparently incomplete and not uniting with the posterior cingulum; M$_{1-2}$ narrower transversely; crown of cheek teeth apparently slightly flatter topped; masseter muscle scar perhaps less anterior in position. Wilson (1940c) noted that all of these characters are subject to individual variation but considered the flattened occlusal surfaces of the teeth to be the most important difference and to represent a more derived evolutionary stage. The upper molars described herein are less worn than the previously described upper molars but also exhibit the flatter occlusal surfaces. Black and Sutton (1984) referred all the material from the Pearson Ranch Fauna and the "Ventura County, Sespe Formation" (= Brea Canyon Local Fauna) to *P. milleri*, presumably because the differences between the specimens from the Sespe Formation and type and topotypic material from the Myton Member of the Uinta Formation in Utah are minor. Until much larger samples are available and intraspecific variation in the Sespe Formation samples can be thoroughly analyzed, the specimens from the Pearson Ranch Local Fauna are referred to *P.* sp., aff. *P. milleri.*

Wilson (1940c) identified an upper molar [LACM(CIT) 2224] from LACM(CIT) loc. 207 as *Pareumys* sp. and stated that it differs from the Pearson Ranch specimens in having a more distinct groove between the protocone and hypocone, less fusion of the metaloph and the posterior cingulum, and more discrete cusps. The M$^1$ described herein closely matches this tooth in size, metaloph morphology, and the presence of a distinct groove between the protocone and hypocone. The characters that Wilson (1940c) used to differentiate the upper molar from LACM(CIT) loc. 207 and those from the Pearson Ranch Local Fauna are probably not reliable because they appear to be the result of different stages of wear. Therefore, LACM(CIT) 2224 from LACM(CIT) loc. 207 is herein tentatively referred to *P.* sp., aff. *P. milleri.*

Wilson (1940c) also identified fragmentary material, including several lower molars from LACM(CIT) loc. 202 as *Pareumys* sp. These specimens, though similar in size, exhibit minor morphological differences relative to comparable material of *P.* sp., aff. *P. milleri,* from the Pearson Ranch Local Fauna. It is also possible that these specimens and the Pearson Ranch specimens are conspecific; however, confirmation must await better material.

Lillegraven (1977) identified specimens from the Camp San Onofre Local Fauna at Camp Pendleton as *Pareumys* sp. and noted that they differed from *P.* sp., aff. *P. milleri,* of the Pearson Ranch Local Fauna in having slightly less fusion of the metaloph and the posterior cingulum. At that time, only two well worn molars of *P.* sp., aff. *P. milleri,* had been described (Wilson, 1940c). The molars of *P.* sp., aff. *P. milleri,* described herein are less worn and the metaloph and the protoloph show less fusion, indicating this character may vary with wear. The Pearson Ranch specimens are slightly larger than those from Camp Pendleton.

The sample of *Pareumys* sp., aff. *P. milleri,* from the Pearson Ranch and Brea Canyon Local Faunas, *Pareumys* sp. from the Brea Canyon Local Fauna at LACM(CIT) loc. 202, and *Pareumys* sp. from the Camp San Onofre Local Fauna appear to represent allied populations that may be conspecific or represent a group of closely related species. These taxa differ from the more primitive *Pareumys* sp., near *P. grangeri* Burke (Wilson, 1940c) from the Friars and Mission Valley Formations in the San Diego area, in having the following characters: larger teeth; metaloph bends toward the posterior cingulum with a greater tendency to fuse with the cingulum; cheek teeth exhibit greater hypsodonty and more completely developed lophs.

## LOCAL FAUNAS

Stock (1932, 1933a,b,c,d, 1934a,b,c,d, 1935a,b,c,d, 1936a,b,c, 1939, 1948) was the first to define the fossil land mammal assemblages from the Sespe Formation in Simi Valley, where he recognized two faunas—the Tapo Ranch and Pearson Ranch Faunas. The Tapo Ranch Fauna included the assemblages from LACM(CIT) locs. 127, 151, 202, and 207, which are present low in the Brea Canyon section, and from LACM(CIT) locs. 180 and 217 in Dry Canyon. The Pearson Ranch Fauna included the assemblages from LACM(CIT) locs. 128, 145, 146, 147, 148, 149, and 150. Stock (1948) placed the Pearson Ranch localities approximately 183 to 214 m (600 to 700 ft) stratigraphically above the Tapo Ranch localities; however, the complexity of the stratigraphic section resulting from faulting was not recognized at the time.

Golz (1976) and Golz and Lillegraven (1977), realizing the stratigraphic relations of the localities in Dry and Brea Canyons were uncertain and that each area produced faunas with differing taxa, divided the Tapo Ranch Fauna into two local faunas—the Brea Canyon Local Fauna, which includes the assemblages from LACM(CIT) locs. 127, 151, 152, 154, 202, and 207, and the Tapo Canyon Local Fauna, which includes the assemblages from LACM(CIT) locs. 180 and 217. Unfortunately, LACM(CIT) locs. 180 and 217, which produced the majority of specimens comprising the Tapo Canyon Local Fauna, are not in Tapo Canyon, but in Dry Canyon, the first large canyon west of Tapo Canyon. However, to maintain nomenclatural stability, the name Tapo Canyon Local Fauna is retained.

Extensive fieldwork conducted for the present study reveals that LACM(CIT) locs. 180 and 217 are located very low in the lower part of the middle member and are from a stratigraphic level within 20 m of bed CS1 in Brea Canyon. The Tapo Canyon Local Fauna is redefined to include not only the assemblages from LACM(CIT) locs. 180 and 217, but also those from bed CS1 in Brea Canyon. The Tapo Canyon Local Fauna is stratigraphically the lowest and, therefore, the oldest local fauna from Simi Valley (Fig. 4).

Golz (1976) considered the Pearson Ranch Fauna a local fauna because it is more restricted geographically and stratigraphically than a fauna. The Pearson Ranch Local Fauna is divided here into two local faunas that are stratigraphically and taxonomically distinct. The name Pearson Ranch Local Fauna is retained for nomenclatural stability but is redefined to include only the assemblages from the localities that are present in bed SS15 and above. The redefined Pearson Ranch Local Fauna still includes the assemblage from LACM(CIT) loc. 150, the "type assemblage" of the Pearson Ranch Fauna of Stock (1932). The assemblages from beds CS8 through CS14, which lie below the Pearson Ranch Local Fauna, are reassigned to the Strathern Local Fauna (new). The stratigraphic relations of the local faunas discussed above are shown in Figure 4, and the stratigraphic ranges of the taxa comprising these local faunas are presented in Table 1.

### TAPO CANYON LOCAL FAUNA

The Tapo Canyon Local Fauna includes the assemblages from LACM(CIT) locs. 180 and 217 in Dry Canyon, along with those from the lowermost Brea Canyon localities—LACM(CIT) loc. 154 and LACM locs. 5621 through 5623 (Fig. 4). The Tapo Canyon Local Fauna is characterized by the restricted stratigraphic ranges of the following species: *Apatemys downsi* Gazin, 1958; *Miacis? hookwayi* Stock, 1934c; *Craseops sylvestris* Stock, 1934b; *Phenacolemur* sp., cf. *P. shifrae* Robinson, 1968; *Dilophodon* sp.; *Leptoreodon edwardsi; Tapomys tapensis* (Wilson, 1940a); *Leptotomus* sp., cf. *L. caryophilus* Wilson, 1940a; *Leptotomus* sp., cf. *L. leptodus* (Cope, 1873); *Ischyrotomus* sp., cf. *I. compressidens* (Peterson, 1919); *Microparamys* sp. D; *Eohaplomys tradux* Stock, 1935a. Mason (1988, unpublished) has also reported a new species of *Simimeryx* from the Tapo Canyon Local Fauna, which is the first Uintan record of the genus.

### BREA CANYON LOCAL FAUNA

The Brea Canyon Local Fauna is comprised of the assemblages from beds CS2 through CS6, which lie from about 50 to 100 m above the highest strata containing the Tapo Canyon Local Fauna, and includes the assemblages from LACM(CIT) locs. 127, 151, 152, 202, and 207, and other LACM and UCMP localities (see Fig. 4). The Brea Canyon Local Fauna is characterized by the restricted stratigraphic ranges of the following species: *Macrotarsius roederi* n. sp.; *Protylopus* sp., cf. *P. petersoni* Wortman, 1898; *Protylopus stocki* Golz, 1976; *Protylopus? robustus* Golz, 1976; *Protylopus?* sp., cf. *P.? robustus; Protylopus?* sp., aff. *P.? robustus; Leptoreodon pusillus; Mytonomys burkei; Rapamys fricki; Tapomys* sp.; *Eohaplomys matutinus* Stock, 1935a; *Eohaplomys serus* Stock, 1935a.

### STRATHERN LOCAL FAUNA

The Strathern Local Fauna (new) is comprised of the assemblages from beds CS8 through CS14, which lie from about 200 to 300 m above the highest strata containing the Tapo Canyon Local Fauna, and includes the assemblages from LACM(CIT) loc. 128; LACM locs. 5633, 5634, and 5636; and probably LACM(CIT) loc. 149 and UCMP loc. V-87156 (Fig. 4). The Strathern Local Fauna is a transitional fauna that contains taxa typical of both the late Uintan Brea Canyon Local Fauna and the early Duchesnean Pearson Ranch Local Fauna. Only two species are restricted to the local fauna, *Leptoreodon* sp., cf. *L. pusillus*, and *Mytonomys* sp., cf. *M. mytonensis*. However, the Strathern Local Fauna is also characterized by the first appearances of *Simimeryx hudsoni* Stock, 1934d, in bed CS8 and *Protoreodon pacificus* Golz, 1976, in bed CS13, and the last occurrences of *Protoreodon "pumilus"* in bed CS13 and *Dyseolemur pacificus* in bed CS14. The presence of a primitive new species of *Simimeryx* in the underlying Tapo Canyon Local Fauna (Mason, 1988) indicates the earliest appearance of *Simimeryx hudsoni* in bed CS8 represents an autochthonous speciation event.

The Strathern Local Fauna differs from the Pearson Ranch Local Fauna by the apparent lack of the following genera: *Hyaenodon, Amynodontopsis, Duchesneodus, Eotylopus, Presbymys.*

## PEARSON RANCH LOCAL FAUNA

The Pearson Ranch Local Fauna (restricted) is comprised of the assemblages from the upper half of bed SS15 through bed SS22, which lie from about 315 to 475 m above the highest strata containing the Tapo Canyon Local Fauna, and includes the assemblages from LACM(CIT) locs. 145, 146, 147, 148, and 150 and other LACM and UCMP localities (see Fig. 4).

During field investigations conducted for this study, four new localities (LACM 5611 through 5614) were found at the head of the southeastern fork of the small canyon near the lower east side of Alamos Canyon. The most productive site (LACM loc. 5611) is in the lowest mottled red-gray claystone bed of the southeast-facing exposure. Locality LACM(CIT) 179 is in the northwest-facing exposure of this small canyon (Fig. 1). The original sample of fossils from LACM(CIT) loc. 179 was either lost or misplaced when transferred from CIT to LACM. The assemblages from LACM(CIT) loc. 179 and LACM locs. 5611 through 5614 are included in the Pearson Ranch Local Fauna because the strata that yielded these assemblages lie above the western extension of the Strathern fault and can be traced to a stratigraphic interval in west Brea Canyon containing beds CS15 through CS18.

The Pearson Ranch Local Fauna is characterized by the restricted stratigraphic ranges of *Chumashius balchi* Stock, 1933d; *Hyaenodon vetus* Stock, 1933a; *Hyaenodon venturae* Mellett, 1977; *Amynodontopsis bodei* Stock, 1933c; *Duchesneodus californicus* (Stock, 1935d); *Protylopus pearsonensis* Golz, 1976; *Eotylopus* sp.; and *Presbymys lophatus* Wilson, 1949. The earliest appearance of *Hyaenodon, Amynodontopsis,* and *Duchesneodus,* taxa that were widespread during the Duchesnean in western North America, may represent an immigration event arising from Asia (Krishtalka *et al.*, 1987).

## BIOSTRATIGRAPHY

A detailed biostratigraphic summary of the Eocene fossil mammal taxa from Simi Valley is presented in Table 1. Certain taxa that are common throughout the section, or are biostratigraphically significant, are discussed below.

The insectivores *Sespedectes singularis* Stock, 1935c, and *Proterixoides davisi* Stock, 1935c, are present throughout the Brea Canyon section. Novacek (1985) reported that combined samples of these species lumped from the Pearson Ranch and the Brea Canyon Local Faunas exhibit rather high coefficients of variation, but it is not possible to recognize any consistent morphologic differences that could be used to separate distinct species within these samples. The pantolestid *Simidectes merriami* Stock, 1933b, is recorded only from the Pearson Ranch Local Fauna at LACM(CIT) loc. 150 (bed CS20).

Primates are relatively rare in the Sespe Formation. *Chumashius balchi* is present only in the Duchesnean Pearson Ranch Local Fauna at LACM(CIT) locs. 146 (bed SS15) and 150 (bed CS20). *Dyseolemur pacificus,* previously recorded from the late Uintan Brea Canyon and Tapo Ranch Local Faunas, is now also recorded from the latest Uintan or earliest Duchesnean Strathern Local Fauna. *Macrotarus roederi* n. sp. is known only from the holotype, which was found in bed CS3 (Brea Canyon Local Fauna).

Creodonts and carnivores are relatively rare in the Sespe Formation. *Hyaenodon* first appears in bed CS20 at LACM(CIT) loc. 150. *Hyaenodon* has been recorded from Duchesnean to Arikareean faunas in the mid-continental United States (Savage and Russell, 1983), and its earliest appearance is considered diagnostic of the early Duchesnean (Wilson, 1986; Krishtalka *et al.*, 1987). *Miacis? hookwayi* Stock, 1934c, is restricted to the Tapo Canyon Local Fauna. *Tapocyon occidentalis* Stock, 1934c, previously thought to be restricted to the Tapo Canyon Local Fauna (Mason, 1988), was discovered in bed CS3 during the present study, extending its range upward into the Brea Canyon Local Fauna. *Procyonodictis progressus* (Stock, 1935b) is recorded from the Tapo Canyon and Brea Canyon Local Faunas.

Amynodonts and brontotheres appear to be more abundant in the Duchesnean strata of Simi Valley than in the Uintan. *Amynodontopsis* first appears in bed SS16 and is also present in beds SS18 through CS20. *Amynodontopsis* is also recorded from Duchesnean faunas in South Dakota, Texas, and Utah. *Duchesneodus* first appears in the upper half of bed

SS15 and continues upward into bed SS22. *Duchesneodus* was widely distributed in western North America (California, New Mexico, South Dakota, Texas, Utah) during the middle and late Eocene and, like *Amynodontopsis,* is restricted to the Duchesnean (Lucas *et al.,* 1981; Wilson and Schiebout, 1981; Wilson, 1986; Krishtalka *et al.,* 1987). For these reasons, the first local appearances of *Duchesneodus* and *Amynodontopsis* can be used for correlating Duchesnean land mammal assemblages.

Artiodactyls are one of the most common groups from the Sespe Formation in Simi Valley. *Simimeryx hudsoni* first appears in bed CS8 and its abundance increases up section, becoming the predominant artiodactyl in beds CS13 through CS20. *Eotylopus* first appears in bed CS20 at LACM(CIT) loc. 150.

Golz (1976) referred the agriochoerid specimens from the Uintan of Simi Valley to *Protoreodon pumilus* (Marsh, 1875), whereas he referred the smaller, more derived specimens from the Duchesnean to *Protoreodon pacificus.* It must be noted that the taxonomic status of *P. pumilus* is a matter of controversy. Wilson (1971) considered the taxon a species group; however, Lander (in lit.) does not consider the specimens referred to *P. pumilus* by Wilson (1971) to be the same species as the holotype for *P. pumilus,* instead assigning them to *Protoreodon annectens* (Scott, 1899). Lander (in lit.) refers specimens from the Brea Canyon Local Fauna to *P. annectens tardus* Scott, 1945, and those from the Strathern and Pearson Ranch Local Faunas to *P. annectens pacificus. Protoreodon pacificus* can be easily distinguished from *P. pumilus* by its smaller size, narrower premolars, and more progressive premolar–molar series (Golz, 1976). Moreover, specimens of *P. pumilus,* identified herein as *P. "pumilus"*, and *P. pacificus* occur together at LACM(CIT) loc. 128, which further affects the issue of their specific or subspecific status. *Protoreodon "pumilus"* is recorded from bed CS13 (Strathern Local Fauna) and from stratigraphically lower in the section at LACM(CIT) locs. 127, 202, and 207 (Brea Canyon Local Fauna). *Protoreodon pacificus* is the characteristic agriochoerid from the Duchesnean of Simi Valley and first appears in bed CS13.

*Leptoreodon* sp., cf. *L. pusillus,* is present in bed CS13 at LACM(CIT) loc. 128 (Strathern Local Fauna) and is closely related to *P. pusillus,* which is present in bed CS6 at LACM(CIT) loc. 5620 (Brea Canyon Local Fauna). *Leptoreodon stocki* n. sp. is present in the Tapo Canyon, Brea Canyon, Strathern, and Pearson Ranch Local Faunas.

Rodents from the Pearson Ranch Local Fauna are represented by relatively small samples compared to those from other Duchesnean and Uintan assemblages in southern California. *Presbymys lophatus* has only been recovered from CS20 at LACM(CIT) loc. 150. *Pareumys* sp., aff. *P. milleri,* is recorded from the Brea Canyon and Pearson Ranch Local Faunas. *Rapamys* is now recorded from the Pearson Ranch Local Fauna, and this record extends the range of the genus into the Duchesnean. *Microparamys tricus* (Wilson, 1940a) first appears in bed CS15 and is restricted to the Duchesnean Pearson Ranch Local Fauna. Mason (1988) referred a specimen (UCMP 132048) from LACM(CIT) loc. 149 to *Leptotomus* sp., cf. *L. mytonensis* (Cope, 1873), and this specimen is herein referred to *Mytonomys* sp., cf. *M. mytonensis,* as recognized by Korth (1988).

## DUCHESNEAN LAND MAMMAL AGE CHARACTERIZATION

Wood *et al.* (1941) based the Duchesnean "North American Provincial Age", now regarded as a land mammal age, on assemblages from the Duchesne River Formation of Utah and included the Pearson Ranch Fauna of Simi Valley as a correlative fauna. Kay (1934) originally recognized three fossiliferous horizons within the Duchesne River Formation. In ascending order, these horizons and their respective faunas were referred to as the Randlett, Halfway, and Lapoint. Andersen and Picard (1972) defined three members within the Duchesne River Formation, including the Brennan Basin (= Randlett and lower Halfway Horizons), Dry Gulch Creek (= upper two-thirds of Halfway Horizon), and the Lapoint Members (= Lapoint Horizon). The Lapoint Member and the upper portion of the Dry Gulch Creek Member are not highly fossiliferous, and unfortunately, detailed biostratigraphic information is lacking (Black and Dawson, 1966a; Emry, 1981).

The Duchesnean is not well defined, and its validity as a land mammal age is the subject of controversy. Scott (1945) regarded the Randlett, Halfway, and Lapoint Faunas as younger than the faunas of the Uinta Formation and referred these faunas to the Oligocene without reference to land mammal ages. Gazin (1955) considered the Randlett Fauna to be Uintan and the Halfway and Lapoint Faunas to be Duchesnean in age. Clark *et al.* (1967) and Tedford (1970) restricted the Duchesnean to the assemblages from the Lapoint Member and its correlatives, whereas Emry (1981) suggested that the Duchesnean be regarded as a subage of the Chadronian and referred the Lapoint and Halfway Faunas to the earliest Chadronian. Wilson (1977) did not recognize the Duchesnean in an early study of the faunas from Trans-Pecos, Texas, but in a later study, Wilson (1986) recognized the Duchesnean as late and early subages of the Uintan and Chadronian, respectively. Storer (1987, 1988), based on a study of small mammals from the La Pelletier Lower Fauna in Saskatchewan, concluded the Duchesnean Land Mammal Age is marked by an O-type episode of rapid faunal turnover caused by a wave of originations.

Whether the Lapoint Fauna should be considered representative of the late Duchesnean subage of the Chadronian or be regarded as belonging to the Duchesnean Land Mammal Age is a matter of interpretation of these ages as originally defined by Wood *et al.* (1941). Although it is beyond the scope of this paper to resolve the Duchesnean-Chadronian controversy, following Wood *et al.* (1941) the Lapoint Fauna is herein referred to the Duchesnean Land Mammal Age as originally defined, not to a late Duchesnean subage of the Chadronian.

Presently, most authors regard the assemblages from the upper Dry Gulch Creek and Lapoint Members as representing the Duchesnean, and, based on similarities to Uintan faunas, refer the Randlett Fauna of the Brennan Basin Member and Halfway Fauna of the upper Brennan Basin and lower Dry Gulch Creek Members to the Uintan (Gazin, 1955; Black and Dawson, 1966a; Clark *et al.*, 1967; Tedford, 1970; Golz, 1976; Savage and Russell, 1983; Krishtalka *et al.*, 1987). However, Mason (1988) provided the most recent faunal list of the assemblage from the Dry Gulch Creek Member, reviewed the stratigraphic provenance of each taxon within this member, and concluded that it is premature to exclude this assemblage from the Duchesnean. This would suggest that the Halfway Fauna, in part, could be Duchesnean; however, only precise stratigraphic collecting from the Dry Gulch Creek Member will determine its age.

Radiometric dates associated with Duchesnean faunas are meager. The Lapoint Fauna lies above an ashy siltstone that occurs at the contact of the Lapoint and Dry Gulch Creek Members and is dated at 40.4 Ma (McDowell *et al.*, 1973). Krishtalka *et al.* (1987) reported that J.A. Wilson redated this ash, resulting in a date of 40.6 Ma. A Duchesnean assemblage from Badwater locality 20 in the Badwater Creek area of Wyoming is associated with a tuff dated at 42.3 ± 1.4 Ma (Black, 1969). Berggren *et al.* (1985) correlate the Duchesnean with the late middle to late Eocene and consider it to be 42 to 37–38 Ma in age.

Krishtalka *et al.* (1987) defined the lower boundary of the Duchesnean by the first appearances of *Hyaenodon, Duchesneodus, Hyracodon, Agriochoerus, Brachyhyops, Simimeryx,* and *Poabromylus* and suggested that some of these taxa may represent an immigration event from Asia similar in magnitude to faunal events that have been used to define other Eocene land mammal age boundaries. However, the presence of *Simimeryx* in the late Uintan Tapo Canyon Local Fauna (Mason, 1988) eliminates the first appearance of this genus as diagnostic of the Duchesnean. Wilson (1986) characterized the Duchesnean by the first appearances of *Hyaenodon, Daphoenus, Duchesneodus, Hyracodon, Amynodontopsis, Brachyhyops, Agriochoerus, Poabromylus,* and *Eotylopus* and the last occurrences of *Hessolestes, Simidectes, Harpagolestes, Duchesneodus, Amynodontopsis, Hyopsodus, Diplobunops,* and *Simimeryx.*

## DUCHESNEAN OF SIMI VALLEY

A comprehensive biostratigraphic record of superposed, fossil-bearing strata that cross the Uintan–Duchesnean boundary in Simi Valley is presented in Table 1. The Duchesnean of Simi Valley is characterized by the first appearances of *Chumashius balchi, Hyaenodon vetus, H. venturae, Duchesneodus californicus, Amynodontopsis bodei, Protylopus pearsonensis, Eotylopus* sp., and *Presbymys lophatus.*

Table 16 lists the mammalian genera found in the late Uintan and Duchesnean assemblages of southern California and their combined Pacific Coast and mid-continental temporal distributions. Of 38 genera represented in southern California, two are restricted to (*Duchesneodus, Amynodontopsis*), four first appear in (*Hyaenodon, Duchesneodus, Amynodontopsis, Eotylopus*), and 11 last occur in the Duchesnean (*Simidectes, Sespedectes, Proterixoides, Leptoreodon, Protylopus, Simimeryx, Rapamys, Pareumys, Presbymys, "Namatomys", Simimys*).

## SUBDIVISIONS OF THE DUCHESNEAN

Many authors have correlated the Pearson Ranch Local Fauna with the Lapoint Fauna (for example, Wood *et al.*, 1941; Black and Dawson, 1966a; Tedford, 1970; Golz, 1976; Emry, 1981; Savage and Russell, 1983); however, Wilson (1986) presented evidence for assigning the Lapoint Fauna to a younger age than the Pearson Ranch Local Fauna.

Wilson (1986) characterized the early Duchesnean by the common occurrences of *Simidectes, Hyaenodon, Duchesneodus,* and *Amynodontopsis,* and the late Duchesnean by the common occurrences of *Hyaenodon, Duchesneodus, Hyracodon, Brachyhyops,* and *Poabromylus.* Wilson (1986) assigned the Skyline Local Fauna (Agua Fria-Green Valley area, Trans-Pecos, Texas), Pearson Ranch Local Fauna [LACM(CIT) loc. 150], and the assemblages from Badwater locality 20 and the Wood locality (Badwater area, Wyoming) to the early Duchesnean, and the Lapoint Fauna and the Porvenir Local Fauna (Vieja-Ojinaga area, Trans-Pecos, Texas) to the late Duchesnean. The Porvenir Local Fauna contains many taxa not recorded from the Lapoint Member but, like the Lapoint Fauna, shows a greater similarity to faunas of Chadronian than to those of Uintan age (Wilson, 1986, fig. 5).

The Lapoint Fauna contains *Hyaenodon, Duchesneodus, Hyracodon, Brachyhyops, Simimeryx,* and *Poabromylus.* Of these taxa, only *Hyaenodon, Duchnesneodus,* and *Simimeryx* are present in the Pearson Ranch Local Fauna. Wilson's (1986) conclusion that the Pearson Ranch Local Fauna is older than the Lapoint Fauna or the Porvenir Local Fauna is further supported herein by the identification of *Leptoreodon* from the Pearson Ranch Local Fauna. *Leptoreodon* is common in Uintan assemblages but is not present in the Lapoint Fauna or Porvenir Local Fauna. Furthermore, *Hydracodon* and *Brachyhyops,* which are also found in Chadronian assemblages, are not recorded from the Pearson Ranch Local Fauna. These data strongly suggest a younger age for the Lapoint Fauna. For this reason, the Lapoint Fauna is herein considered late Duchesnean in age.

The Pearson Ranch Local Fauna is present in the upper half of bed SS15 through bed SS22 and is characterized by the first appearances of *Duchesneodus californicus, Amynodontopsis bodei, Hyaenodon venturae, Hyaenodon vetus, Protylopus pearsonensis, Eotylopus* sp., and *Presbymys lophatus* and the occurrences of *Sespedectes singularis, Proterixoides davisi, Simidectes merriami, Chumashius balchi, Triplopus? woodi* Stock, 1936c, *Protoreodon pacificus, Leptoreodon stocki* n. sp., *Simimeryx hudsoni, Microparamys tricus, Pareumys* sp., aff. *P. milleri, Griphomys alecer* Wilson, 1940b, and *Simimys simplex* (Wilson, 1935a). The Pearson Ranch Local Fauna is older than the Lapoint Fauna and Porvenir Local Fauna, as indicated by its containing a greater number of taxa having affinities with those of the Uintan than the Chadronian. The Pearson Ranch Local Fauna is herein regarded as early Duchesnean in age.

The Strathern Local Fauna is present in beds CS8 through CS14 and is characterized by the first appearances of *Simimeryx hudsoni* and *Protoreodon pacificus,* the last occurrences of *Dyseolemur pacificus, Protoreodon "pumilus"*, and *Leptoreodon* sp., cf. *L. pusillus,* and by the occurrences of *Sespedectes singularis, Proterixoides davisi, Triplopus? woodi, Leptoreodon stocki* n. sp., and *Mytonomys* sp., cf. *M. mytonensis.* The fauna is of transitional Uintan–Duchesnean age, with a combination of species typical of the late Uintan (*D. pacificus, P. "pumilus"*) and the Duchesnean (*P. pacificus, S. hudsoni*). The fauna lacks taxa (*Hyaenodon, Duchesneodus, Amynodontopsis, Eotylopus, Presbymys*) diagnostic of the overlying early Duchesnean Pearson Ranch Local Fauna. The Strathern Local Fauna lies immediately below the Pearson Ranch Local Fauna and about 100 m above the late Uintan Brea Canyon Local Fauna. The Strathern Local Fauna does not contain the first appearance of any diagnostic Duchesnean genus and should be regarded as latest Uintan. The Uintan–Duchesnean boundary can be considered to be at the first appearance of the diagnostic Duchesnean taxon *Duchesneodus* in bed SS15; however, the sample size of *Duchesneodus* from Simi Valley is small, and the apparent absence of this genus in the Strathern Local Fauna is not unequivocal. Furthermore, *Triplopus? woodi* is present in the Pearson Ranch and Strathern Local Faunas but not in the late Uintan Brea Canyon Local Fauna. It is premature to restrict the Strathern Local Fauna to the Uintan, and this fauna could be latest Uintan or earliest Duchesnean.

## UINTAN LAND MAMMAL AGE

The Uinta Formation of the Uinta Basin in Utah is the stratotype of the Uintan age (Wood *et al.*, 1941). Wood (1934) divided the Uinta Formation into the Wagonhound and the overlying Myton Members. The Duchesne River Formation overlies and, in its lower 325 m (1064 ft), interfingers with the Myton Member of the Uinta Formation (Andersen and Picard, 1972).

The characteristic Uintan taxa from southern California are *Procyonodictis, Tapocyon, Craseops, Stockia, Dilophodon, Amynodon, Tapochoerus, Merycobunodon, Pöebrodon, Tapomys,* and *Eohaplomys.*

Krishtalka *et al.* (1987) discussed the history of the faunal divisions of the Uinta Formation. The Uintan is currently subdivided into early and late segments. The early Uintan is typified by the assem-

**Table 16. Mammalian genera found in late Uintan and Duchesnean assemblages in southern California, with combined geochronologic ranges along the Pacific Coast and in the mid-continental United States (Duch. = Duchesnean; Chad. = Chadronian).**

| Genera | Uintan | Duch. | Chad. |
|---|---|---|---|
| *Peratherium* | ——— | ——— | ——— |
| *Peradectes* | ——— | ——— | ——— |
| *Mytonolagus* | ——— | ——— | |
| *Simidectes* | ——— | ——— | |
| *Apatemys* | ——— | ——— | |
| *Hyaenodon* | | ——— | ——— |
| *Procyonodictis* | ——— | | |
| *Miacis* | ——— | ——— | ——— |
| *Tapocyon* | ——— | | |
| *Sespedectes* | ——— | ——— | |
| *Proterixoides* | ——— | ——— | |
| *Craseops* | ——— | | |
| *Dyseolemur* | ——— | —? | |
| *Chumashius* | ——— | ——— | ——— |
| *Macrotarsius* | ——— | ——— | ——— |
| *Duchesneodus* | | ——— | |
| *Dilophodon* | ——— | | |
| *Amynodon* | ——— | | |
| *Amynodontopsis* | | ——— | |
| *Tapochoerus* | ——— | | |
| *Protoreodon* | ——— | ——— | ——— |
| *Leptoreodon* | ——— | ——— | |
| *Poebrodon* | ——— | | |
| *Protylopus* | ——— | ——— | |
| *Eotylopus* | | ——— | ——— |
| *Simimeryx* | ——— | ——— | |
| *Leptotomus* | ——— | ——— | ——— |
| *Mytonomys* | ——— | ——— | ——— |
| *Tapomys* | ——— | | |
| *Microparamys* | ——— | ——— | ——— |
| *Rapamys* | ——— | ——— | |
| *Ischyrotomus* | ——— | ——— | ——— |
| *Pareumys* | ——— | ——— | |
| *Presbymys* | ——— | ——— | |
| *"Namatomys"* | ——— | ——— | |
| *Griphomys* | ——— | ——— | ——— |
| *Eohaplomys* | ——— | | |
| *Simimys* | ——— | ——— | |

blages from the Wagonhound Member, and the late Uintan by the assemblages from the Myton Member and the Brennan Basin and lower Dry Gulch Creek Members of the Duchesne River Formation (Krishtalka *et al.*, 1987). However, as noted above, the fossil record from the Dry Gulch Creek Member is poor, and Mason (1988) considers its age uncertain. In ascending stratigraphic order, the localities that produced most of the taxa from the Myton Member are Leland Bench Draw, Myton Pocket, and Leota Ranch.

Krishtalka *et al.* (1987) characterize the early Uintan by the first appearances of *Epihippus, Metarhinus, Dolichorhinus,* hyracodonts, amynodonts, *Mytonomeryx, Bunomeryx, Hylomeryx, Mesomeryx, Achaenodon,* agriochoerids, oromerycids, and protoptychids and the last occurrences of *Metarhinus, Telmatherium,* taeniodonts, uintatheres, and *Protoptychus.* Krishtalka *et al.* (1987) characterize the late Uintan by the first appearances of *Domnina, Simidectes, Thylacaelurus, Procyonodictis, Prodaphoenus, Colodon, Pöebrodon,* and *Epitriplopus. Tapocyon* (Stock, 1934c; Dawson, 1980), *Chumashius* (Robinson, 1968; Krishtalka, 1978; Lillegraven, 1980), and *Simimeryx* (Mason, 1988) also have first appearances in the late Uintan.

## AGE AND CORRELATION OF MIDDLE AND LATE EOCENE LAND MAMMAL ASSEMBLAGES

The Eocene fossil mammal assemblages from the lower part of the middle member of the Sespe Formation in Simi Valley can be correlated with other middle and late Eocene assemblages from California, Texas, Wyoming, and Utah.

### CALIFORNIA

Golz (1976), Golz and Lillegraven (1977), and Lillegraven (1980) characterized the Eocene land mammal assemblages from the San Diego area in southern California. These faunal assemblages include the late Bridgerian or early Uintan assemblage from the Ardath Shale, and the early Uintan assemblages from the Friars Formation, Stadium Conglomerate, and the Mission Valley Formation. However, Walsh (1987), in a study of the southern outcrops of the Mission Valley Formation in the San Diego area, has suggested these assemblages be divided into two faunas as follows: the early Uintan Poway Fauna from the Friars Formation in the greater San Diego area and from the outcrops of the Mission Valley Formation at Rancho Peñasquitos and Rancho Bernardo in the Poway area, and the late Uintan Cloud 9 Fauna from the southern outcrops of the Mission Valley Formation in the eastern part of the greater San Diego area.

Three local faunas, which range in age from late Uintan to Duchesnean, were reported from the Santiago Formation in the Carlsbad area by Golz (1976), Golz and Lillegraven (1977), and Lillegraven (1977, 1980). These faunas include the Laguna Riviera, Camp San Onofre, and the Chestnut Avenue Local Faunas. The ages of the assemblages from the Carlsbad area and the Cloud 9 Fauna are reassessed below in light of the results of the present study.

During the present study, *Dyseolemur pacificus, Protoreodon "pumilus"*, and *Leptoreodon,* taxa previously recorded only from late Uintan assemblages in the Carlsbad area and Simi Valley, were also found in the latest Uintan or earliest Duchesnean Strathern Local Fauna. Moreover, Golz and Lillegraven (1977) and Lillegraven (1977, 1980) have identified *Chumashius balchi, Simimeryx* sp., cf. *S. hudsoni,* and *Microparamys tricus* in the Camp San Onofre Local Fauna, which they considered late Uintan in age.

In Simi Valley, *S. hudsoni* is recorded only from the Strathern and Pearson Ranch Local Faunas, and *C. balchi* and *M. tricus* only from the Pearson Ranch Local Fauna. In the Carlsbad area, *C. balchi* and *M. tricus* are only present at UCMP loc. V-72088 (Camp San Onofre Local Fauna), and *Simimeryx* only at UCMP locs. V-72088 and V-71053 (Chestnut Avenue Local Fauna). The Camp San Onofre Local Fauna is from an isolated exposure of the Santiago Formation on the Camp Pendleton Marine Corps Base, and its stratigraphic position relative to the other assemblages in the Santiago Formation is uncertain. Field studies, which were conducted by the author for this study, indicate the Chestnut Avenue Local Fauna is stratigraphically higher in the Santiago Formation than the Laguna Riviera Local Fauna. The assignment of the Camp San Onofre Local Fauna to the late Uintan by Lillegraven (1977, 1980) extended the geologic ranges of *C. balchi* and *M. tricus* downward. Golz (1976) considered the Chestnut Avenue Local Fauna to be late Uintan or Duchesnean.

Lillegraven (1977) regarded the Camp San Onofre Local Fauna as a correlative of the Uintan assemblages from Simi Valley because of the joint occurrences of the rodent genera *Microparamys, Griphomys,* and *Pareumys,* and possibly the joint occurrences of three species of these genera (*M. tricus, G. alecer, Pareumys* sp.). However, these genera are also present in the early Duchesnean Pearson Ranch Local Fauna. Furthermore, *M. tricus* is actually restricted to the Pearson Ranch Local Fauna, and *G. alecer* is also recorded in the Pearson Ranch Local Fauna (Black and Sutton, 1984). The diagnostic dental character (fusion of lingual end of metaloph to posterior cingulum), which Lillegraven (1977) used to demonstrate the sample of *Pareumys* sp. from the Camp San Onofre Local Fauna as being distinct from and less derived than the sample of *P.* sp., aff. *P. milleri,* of the Pearson Ranch Local Fauna, is now known to be unreliable because it varies intraspecifically. Moreover, the upper molars from the Pearson Ranch Local Fauna herein assigned to *P.* sp., aff. *P. milleri,* cannot be distinguished from *Pareumys* sp. from the Camp San Onofre Local Fauna on the basis of this character. Lillegraven (1980) later reported *Chumashius* *balchi* and *Dyseolemur pacificus* from the Camp San Onofre Local Fauna. The presence of *D. pacificus* in the Camp San Onofre Local Fauna, a taxon previously reported only from late Uintan assemblages in Simi Valley, appeared to support a late Uintan age assignment. However, *D. pacificus* is now known from the latest Uintan or earliest Duchesnean Strathern Local Fauna, and *C. balchi* is restricted to the early Duchesnean Pearson Ranch Local Fauna.

The Camp San Onofre Local Fauna and the Pearson Ranch Local Fauna share five species (*Proterixoides davisi, Chumashius balchi, Microparamys tricus, Simimys simplex, Griphomys alecer*). The Camp San Onofre Local Fauna has slightly greater affinities with the Pearson Ranch Local Fauna than with the Brea Canyon Local Fauna, which lacks *C. balchi* and *M. tricus.* The Camp San Onofre Local Fauna and the latest Uintan or earliest Duchesnean Strathern Local Fauna are probably correlatives because both contain *D. pacificus* and *Simimeryx* and are transitional faunas with taxa characteristic of the late Uintan and early Duchesnean. The Chestnut Avenue Local Fauna may also be latest Uintan or earliest Duchesnean in age because it contains *S.* sp., cf. *S. hudsoni,* and lies above the late Uintan Laguna Riviera Local Fauna.

The Laguna Riviera, Strathern, and Pearson Ranch Local Faunas contain four species in common (*Simidectes merriami, Proterixoides davisi, Dyseolemur pacificus, Protoreodon "pumilus"*), whereas the Laguna Riviera and the Brea Canyon Local Faunas contain ten species in common [*Peratherium* sp., cf. *P. knighti* McGrew, 1959; *Peradectes californicus* (Stock, 1936a); *Sespedectes singularis; Proterixoides davisi; Dyseolemur pacificus; Protoreodon "pumilus"; Leptoreodon pusillus; Protylopus? robustus; Protylopus* sp., cf. *P. petersoni* Wortman, 1898; *Protylopus stocki*]. The Laguna Riviera and Brea Canyon Local Faunas also contain *Amynodon.*

Golz (1976) correlated the Laguna Riviera Local Fauna with the late Uintan Brea Canyon Local Fauna based on the common occurrences of *D. pacificus* and *P. "pumilus"*, both of which are now known to be present in the latest Uintan or earliest Duchesnean Strathern Local Fauna. However, Lander (in lit., personal communication) considers specimens of *P. "pumilus"* from the Laguna Riviera Local Fauna to be more derived than those of *P. "pumilus"* from the Brea Canyon Local Fauna. Nevertheless, the composition of the Laguna Riviera Local Fauna exhibits a much greater affinity with the late Uintan Brea Canyon Local Fauna than the Strathern or Pearson Ranch Local Fauna and supports Golz's (1976) conclusion that the Laguna Riviera Local Fauna is a correlative of the Brea Canyon Local Fauna and late Uintan in age.

The Tapo Canyon and the Laguna Riviera Local Faunas have five species in common (*Peratherium* sp., cf. *P. knighti; Sespedectes singularis; Proterixoides davisi; Dyseolemur pacificus; Protoreodon "pumilus"*), whereas the Tapo Canyon and the Brea Canyon Local Faunas have seven species in common [*Peratherium* sp., cf. *P. knighti; Sespedectes singularis; Proterixoides davisi; Tapocyon occidentalis; Dyseolemur pacificus; Tapochoerus egressus* (Stock, 1934b); *Leptoreodon stocki* n. sp.]. However, the Tapo Canyon Local Fauna contains at least 13 other species (see above) that do not occur in either the Brea Canyon or Laguna Riviera Local Faunas. Golz (1976) suggested the Tapo Canyon Local Fauna represents an older assemblage than the Laguna Riviera Local Fauna, based on the observation that *Leptoreodon edwardsi* from LACM(CIT) loc. 180 is more primitive than *L. leptolophus* from the Laguna Riviera Local Fauna. Wilson (1949) considered the rodent *Eohaplomys tradux* from the Tapo Canyon Local Fauna to be more primitive than *E. matutinus* and *E. serus* from the Brea Canyon Local Fauna. Golz (1976) considered the faunal differences between the Brea Canyon and Tapo Canyon Local Faunas the result of local environmental differences. It is more likely that these faunal differences reflect age differences because the Tapo Canyon Local Fauna lies about 50 to 100 m below the Brea Canyon Local Fauna and contains species that are more primitive than those from the Brea Canyon Local Fauna. The faunal and stratigraphic evidence indicate the Laguna Riviera and Brea Canyon Local Faunas are younger than the Tapo Canyon Local Fauna.

Walsh (1987) considered the Cloud 9 Fauna from the southern outcrops of the Mission Valley Formation in the San Diego area to show greater similarities with the late Uintan Tapo Ranch Fauna (= Tapo Canyon and Brea Canyon Local Faunas) and late Uintan Laguna Riviera Local Fauna than the early Uintan Poway Fauna. The Cloud 9 and Poway Faunas contain three taxa not found in the Tapo Canyon or Brea Canyon Local Faunas (*Batodonoides powayensis* Novecek, 1976, *Uintasorex* sp., *Protoreodon* sp., cf. *P. parvus* Scott and Osborn, 1887). The Cloud 9 Fauna contains six species in common with the Tapo Canyon and Brea Canyon Local Faunas (*Peratherium* sp., cf. *P. knighti; Peradectes californicus; Sespedectes singularis; Proterixoides davisi; Dyseolemur pacificus; Simimys simplex*). In addition, the Cloud 9 Fauna and Tapo Canyon Local Fauna contain *Apatemys, Microparamys* "sp. D", and *Eohaplomys.* Walsh (1987) considers *Eohaplomys* sp. of the Cloud 9 Fauna to be most closely related to *E. tradux* of the Tapo Canyon Local Fauna. The presence of *Simidectes* in the Cloud 9 Fauna (Walsh, 1987), a taxon whose first appearance is regarded as diagnostic of the late Uintan by Krishtalka *et al.* (1987), further supports a late Uintan age.

The Cloud 9 Fauna and the Laguna Riviera Local Fauna contain only two species in common (*Sespedectes singularis, Dyseolemur pacificus*). Moreover, *P. "pumilus"* from the Laguna Riviera Local Fauna is more advanced than *P.* sp., cf. *P. parvus,* of the Cloud 9 and Poway Faunas (Golz, 1976;

Lander, in lit., personal communication *in* Walsh, 1987). The Cloud 9 Fauna exhibits greater affinities with the Tapo Canyon Local Fauna than with the Brea Canyon and Laguna Riviera Local Faunas; however, the Cloud 9 Fauna is probably slightly older than the Tapo Canyon Local Fauna because it contains species (*B. powayensis; P.* sp., cf. *P. parvus*) elsewhere known only from the early Uintan Poway Fauna. Based on the above data and the observations presented by Walsh (1987), the Cloud 9 Fauna is herein regarded as early late Uintan in age.

Stock (1938) reported the presence of *Teleodus* sp., cf. *T. californicus,* from LACM(CIT) loc. 292, which is in the massive sandstones of the Sespe Formation exposed along upper Sespe Creek, north of Ojai, Ventura County, California. The sample of *Teleodus* from LACM(CIT) loc. 292 is herein referred to *Duchesneodus* sp., cf. *D. californicus,* as recognized by Lucas and Schoch (1982). Fieldwork conducted in the upper Sespe Creek area by the author resulted in the recovery of *Amynodontopsis* from a siltstone overlying LACM(CIT) loc. 292. The assemblage from LACM(CIT) loc. 292 and vicinity, identified herein as the Sespe Creek Local Fauna, is Duchesnean in age and probably a correlative of the Pearson Ranch Local Fauna, based on the common occurrences of *Duchesneodus* and *Amynodontopsis.*

Lindsay (1968) described a rodent assemblage from the Hartman Ranch Local Fauna at UCMP loc. V-5814 in the lower part of the Sespe Formation in the upper Sespe Creek area. Lindsay (1968) reported that the fossil-bearing horizon is in a transitional zone, in which the Sespe Formation interfingers with the underlying marine Coldwater Sandstone. Mason (1988) reported UCMP loc. V-5814 is stratigraphically far below LACM(CIT) loc. 292 and is actually in strata now mapped as Coldwater Sandstone by Vedder *et al.* (1972). Lindsay (1968) correlated the Hartman Ranch Local Fauna, which contains *Pareumys* sp., "*Namatomys*" *fantasma* (Lindsay, 1968), *Griphomys* sp., and *Simimys* sp., with the Tapo Ranch Fauna (= Brea Canyon and Tapo Canyon Local Faunas) and assigned it to the Uintan. Lindsay (1968) considered *Pareumys* sp. and *Simimys* sp. from the Hartman Ranch Local Fauna to be most closely related to *Pareumys* sp. and *Simimys murinus,* respectively, from the Tapo Ranch Fauna. However, the distinctiveness of *Pareumys* sp. from the Tapo Ranch and Brea Canyon Local Faunas and *Pareumys* sp., aff. *P. milleri,* of late Uintan to early Duchesnean age is now questioned (see above). Moreover, Lillegraven and Wilson (1975) analyzed the diagnostic dental characters and measurements of a large sample of *Simimys* from the latest Uintan or earliest Duchesnean Camp San Onofre Local Fauna and found that all species of the genus fit within the range of variation observed in the Camp San Onofre sample. It was concluded that only one species of *Simimys—S. simplex*—is present in southern California. The Hartman Ranch Local Fauna may be late Uintan in age because it occurs well below the Duchesnean Sespe Creek Local Fauna; however, the faunal evidence does not eliminate an early Duchesnean age assignment.

## TEXAS

The Serendipity Local Fauna, from the Agua Fria-Green Valley area in Texas, and the Tapo Ranch and the Brea Canyon Local Faunas have the shared occurrences of *Leptoreodon edwardsi* and *L. pusillus,* respectively (Wilson, 1986). However, *L. pusillus* is also reported from the Whistler Squat Local Fauna in the Agua Fria-Green Valley area, where it is bracketed by K–Ar dates of 44.0 ± 0.9 Ma above, and 46.9 ± 1.1 and 48.6 ± 1.3 Ma below (McDowell, 1979; Stevens *et al.,* 1984; Wilson, 1986). The Serendipity Local Fauna lies above the early Uintan Whistler Squat Local Fauna and the tuff dated at 44.0 ± 0.9 Ma, and below a tuff K–Ar dated at 42.7 Ma (Wilson, 1986). Wilson (1986) considered the Serendipity Local Fauna to be late Uintan in age. The faunal composition suggests the fauna is early late Uintan in age and a correlative of the Cloud 9 Fauna from the greater San Diego area.

Wilson (1986) also correlated the Serendipity Local Fauna with the Candelaria Local Fauna from the Vieja-Ojinaga area in Texas. The Candelaria Local Fauna is bracketed by K–Ar dates of 39.7 ± 1.2 Ma above and 41.2 ± 2 Ma below (Wilson *et al.,* 1968). The radiometric dates bracketing these faunas suggest that the Serendipity Local Fauna is older than Candelaria Local Fauna.

Wilson (1977, 1984, 1986) assigned the Candelaria Local Fauna to the Uintan, based on the presence of *Epihippus* sp., cf. *E. gracilis* Marsh, 1871; *Dilophodon* sp., cf. *D. leotanus* (Peterson, 1931); *Protoreodon petersoni* Gazin, 1955; and *Leptoreodon leptolophus.* The Candelaria and late Uintan Laguna Riviera Local Faunas have the shared occurrence of *Leptoreodon leptolophus.* Wood (1974) considered the rodents of the Candelaria Local Fauna to be late Uintan but post-Myton in age. *Dilophodon* is also present in the late Uintan Tapo Canyon and Laguna Riviera Local Faunas. Lander (in lit.) considers the specimens from the Candelaria Local Fauna, which Wilson (1984, 1986) referred to *Protoreodon petersoni,* to represent a new genus and species of agriochoerid. Lander (in lit.) also considers this new species to be more advanced than species of same genus from late Uintan assemblages of the Myton Member in the Devils Playground area of Utah and assigns the Candelaria Local Fauna to the early Duchesnean. Black (1978) considered the Candelaria Local Fauna Duchesnean in age but older than the Pearson Ranch Fauna and younger than the Tapo Ranch Fauna (= Brea Canyon and Tapo Canyon Local Faunas), the Laguna Riviera Local Fauna, and the Myton Fauna. Krishtalka *et al.* (1987) correlate the Candelaria Local

Fauna with the latest Randlett and Halfway Faunas from the Uinta Formation in Utah.

The Candelaria Local Fauna is a transitional fauna that contains taxa known elsewhere in late Uintan faunas (*Dilophodon, Epihippus, Sthenodectes*); late Uintan and Duchesnean faunas (*Leptoreodon*); and late Uintan, Duchesnean, and Chadronian faunas (*Colodon, Metamynodon, Ischyrotomus, Manitsha*). It is difficult to correlate the Candelaria Local Fauna with the middle and late Eocene faunas of the Pacific Coast; however, this fauna, like the Strathern Local Fauna, may be latest Uintan or earliest Duchesnean in age.

Wilson (1986) correlated the early Duchesnean Pearson Ranch Local Fauna with the Skyline Local Fauna from the Agua Fria-Green Valley area in Texas, based on the common occurrences of *Simidectes, Hyaenodon, Duchesneodus,* and *Amynodontopsis.* The Skyline Local Fauna occurs in the Skyline Channels, directly above a biotite-bearing ash K–Ar dated at 42.7 Ma (Wilson and Schiebout, 1981; Wilson, 1986). The Strathern Local Fauna appears to be slightly older than the Skyline Local Fauna because of the presence of *Dyseolemur* and the apparent lack of *Duchesneodus* and *Hyaenodon.*

The Porvenir Local Fauna from the Vieja-Ojinaga area occurs above the Buckshot Ignibrite (K–Ar dated at 38.6 ± 1.2 Ma) and below the Bracks Rhyolite (K–Ar dated at 37.7 ± 1.2 Ma) (McDowell, 1979). Krishtalka *et al.* (1987) refer the Porvenir Local Fauna to the Duchesnean, whereas Emry *et al.* (1987) regard this local fauna as earliest Chadronian. The Porvenir Local Fauna contains certain taxa (*Mesohippus, Archaeotherium, Pseudoprotoceras, Leptomeryx*) found elsewhere only in Chadronian faunas (Emry *et al.*, 1987). The Porvenir Local Fauna appears to be younger in age than the type Duchesnean Lapoint Fauna, based on its greater similarity to Chadronian faunas. The Porvenir Local Fauna is herein regarded as latest Duchesnean to earliest Chadronian in age.

## WYOMING

Correlation of the Pacific Coast middle and late Eocene land mammal assemblages with those from the Hendry Ranch Member of the Wagon Bed? Formation from the Badwater area in Wyoming is difficult because of differing faunal compositions and the lack of radiometric dates (Black, 1978; Wilson, 1977). Black (1978) concluded the fauna from Badwater localities 5, 6, and 7 correlate best with the late Uintan Myton Fauna of Utah, the Tapo Ranch Fauna (= Brea Canyon and Tapo Canyon Local Faunas), and the Laguna Riviera Local Fauna. The common occurrence of *Tapocyon* in the fauna from Badwater localities 5, 6, and 7 (Dawson, 1980), the Tapo Canyon and Brea Canyon Local Faunas (this report), and the Myton Fauna (Mason, 1988) suggest these faunas are correlatives.

Black (1969, 1978) considered the assemblage from Badwater locality 20, which is associated with a tuff K–Ar dated at 42.3 ± 1.4 Ma, and most probably those from the Badwater Wood and Rodent localities, to be younger than the fauna from Badwater localities 5, 6, and 7 but older than the Pearson Ranch Fauna. The assemblages from Badwater locality 20 and the Wood and Rodent localities have yielded a diverse fauna, which includes *Peratherium, Peradectes, Apternodus, Trogolemur, Chumashius, Macrotarsius, Daphoenus, Epihippus, ?Telmatherium, Diplobunops, Leptotragulus, Poabromylus, Hendryomeryx, Microparamys, Leptotomus, Spurimus, Pareumys, Pseudocylindrodon,* and *Griphomys* sp. (see Black, 1969, 1971, 1974, 1978, 1979; Black and Dawson, 1966b; Dawson, 1974, 1980; Krishtalka, 1978; Krishtalka and Setoguchi, 1977; Krishtalka and Stucky, 1983; Maas, 1985; MacFadden, 1980; Robinson, 1966, 1968; Setoguchi, 1975).

The assemblages from Badwater locality 20 and the Wood and Rodent localities are transitional in age because they contain a combination of late Uintan and Duchesnean taxa; however, the presence of certain taxa (*Apternodus, Daphoenus, Poabromylus, Pseudocylindrodon*) indicates a Duchesnean age for these assemblages. Wilson (1986) assigned the Skyline and Pearson Ranch Local Faunas, and the assemblages from Badwater locality 20 and the Wood locality to the early Duchesnean. A K–Ar date of 42.7 Ma (Wilson and Schiebout, 1981; Wilson, 1986) from an ash lying immediately below the Skyline Local Fauna and the date of 42.3 Ma for the tuff associated with the assemblage from Badwater locality 20 (Black, 1969, 1978) also suggest these assemblages are correlatives. The assemblages from Badwater locality 20 and the Wood and Rodent localities are herein regarded as early Duchesnean and probable correlatives of the Skyline and Pearson Ranch Local Faunas.

## UTAH

The Myton Fauna from the Myton Member of the Uinta Formation and the Randlett Fauna of the Brennan Basin Member of the overlying Duchesne River Formation in Utah are considered late Uintan. The age of the Halfway Fauna, in part from the overlying Dry Gulch Creek Member of the Duchesne River Formation, has been questioned, and its assignment to the Uintan is not unequivocal (see above).

The Myton Fauna appears to correlate with the Randlett Fauna because of shared occurrences of certain species [*Petacemylus progressus* Peterson, 1931; *Protoreodon "pumilus"*; *Mytonomys robustus* (Peterson, 1919)] and genera (*Epihippus, Amynodon, Epitriplopus, Dilophodon, Diplobunops, Leptotomus, Mytonolagus*) (Gazin, 1955; Dawson, 1966; Tedford, 1970; Emry, 1981; Andersen and Picard, 1972; Krishtalka *et al.*, 1987). The Myton Fauna is difficult to correlate with the middle Eocene assemblages from the Pacific Coast and Texas because of the lack of shared species and radiometric dates. The Tapo Canyon and Brea Canyon Local Faunas may correlate with the Myton Fauna based on the joint occurrences of *Tapocyon, Procyonodictis, Protoreodon "pumilus"*, and *Thisbemys.* Furthermore, *Ischyrotomus compressidens* (Peterson, 1919) of the Myton Fauna is very similar to *I.* sp., near *I. compressidens* of the Tapo Canyon Local Fauna.

The Lapoint Fauna of the Duchesne River Formation is younger than the early Duchesnean Pearson Ranch Local Fauna and is regarded herein as late Duchesnean in age (see above).

## SUMMARY

Four Eocene local faunas are now recognized in the lower part of the middle member of the Sespe Formation in Simi Valley, Ventura County, California. The Tapo Canyon Local Fauna is the oldest and is comprised of the assemblages from within about 20 m of bed CS1. The overlying Brea Canyon Local Fauna is present in beds CS2 through CS6. The Strathern Local Fauna (new) is present in beds CS8 through CS14. The Pearson Ranch Local Fauna (restricted) is present in the upper half of bed SS15 through bed SS22.

The biostratigraphic framework developed herein will allow subsequent workers to use the faunas from the Sespe Formation with greater precision when conducting biostratigraphic and evolutionary studies. An ongoing mitigation project at the Simi Valley Landfill by Waste Management of North America, Inc. is resulting in the recovery of stratigraphically superposed samples of small mammals from the Sespe Formation. Future study of these samples will provide additional data on the geologic ranges of taxa from the Sespe Formation and further clarify the Uintan–Duchesnean boundary in Simi Valley.

The study summarized herein documents taxa that had not previously been recorded from the Brea Canyon Local Fauna (*Leptoreodon pusillus; Protylopus*? sp., cf. *P.*? *robustus*) and the range extensions of *Leptoreodon* and *Rapamys* from the late Uintan into the Duchesnean. The present study also resulted in the discovery of two new species: *Leptoreodon stocki,* which is present in the Tapo Canyon, Brea Canyon, Strathern, and the Pearson Ranch Local Faunas, and *Macrotarsius roederi* from the Brea Canyon Local Fauna.

The Brea Canyon and Tapo Canyon Local Faunas are late Uintan in age; however, the Tapo Canyon Local Fauna, which occurs below the Brea Canyon Local Fauna and contains a less derived fauna, is slightly older. The latest Uintan or earliest Duchesnean Strathern Local Fauna is transitional and contains a combination of characteristic Uintan and Duchesnean taxa. The early Duchesnean is characterized by the first appearances of *Hyaenodon, Duchesneodus,* and *Amynodontopsis* and includes the Pearson Ranch Local Fauna. The late Duchesnean is characterized by the first appearances of *Hyracodon, Brachyhyops,* and *Agriochoerus* and the last occurrences of *Duchesneodus* and *Amynodontopsis,* and is represented by the Lapoint Fauna of Utah.

The Eocene faunas from the Sespe Formation appear to correlate with other Eocene assemblages from southern California as follows: the Chestnut Avenue Local Fauna from the Carlsbad area and the Camp San Onofre Local Fauna from Camp Pendleton are probably correlatives of the Strathern Local Fauna; the Laguna Riviera Local Fauna from the Carlsbad area appears to correlate with the Brea Canyon Local Fauna; the Sespe Creek Local Fauna from the upper Sespe Creek area is probably a correlative of the Pearson Ranch Local Fauna; the Hartman Ranch Local Fauna from the upper Sespe Creek area is probably late Uintan in age and may correlate with the Brea Canyon Local Fauna.

The Eocene faunas from the Vieja-Ojinaga area in Texas appear to be related to the Pacific Coast assemblages as follows: the Candelaria Local Fauna may be a correlative of the Strathern Local Fauna; the Porvenir Local Fauna is younger than the Pearson Ranch Local Fauna and is latest Duchesnean or earliest Chadronian in age.

The Eocene assemblages from the Agua Fria-Green Valley area in Texas appear to correlate with the Pacific Coast assemblages as follows: the Whistler Squat Local Fauna is a correlative of the Poway Fauna from the greater San Diego area; the Serendipity Local Fauna is a possible correlative of Cloud 9 Fauna from the greater San Diego area; the Skyline Local Fauna is a correlative of the Pearson Ranch Local Fauna.

The late Uintan assemblages from the Hendry Ranch Member of the Wagon Bed? Formation at Badwater localities 5, 6, and 7 in Wyoming are difficult to correlate with any single local fauna in southern California because of faunal differences. The assemblages from the Hendry Ranch Member at Badwater locality 20 and the Rodent and Wood localities appear to be correlatives with the Pearson Ranch Local Fauna and are early Duchesnean in age.

The Myton Fauna of the Uinta Formation in Utah is difficult to correlate with any local fauna in southern California but appears, in general, to correlate with the Brea Canyon and Tapo Canyon Local Faunas.

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## APPENDIX

Descriptions and stratigraphic horizons of LACM(CIT) localities in the Sespe Formation from Simi Valley, as well as the taxa these localities yielded during the present study.

LACM(CIT) loc. 127. Lat. 34°17′37″N; Long. 118°46′52″W. East side, Brea Canyon, elevation approximately 314 m, bed CS4, middle member, Sespe Formation. LACM(CIT) loc. 127 occurs in a small basin of badlands just west of the canyon containing LACM(CIT) loc. 151 (Fig. 1). Taxa: *Protoreodon* sp.; *Leptoreodon stocki* n. sp.

LACM(CIT) loc. 128. Lat. 34°17′47″N; Long. 118°47′19″W. West side, Brea Canyon, 104 m S 23°W from the top of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 290 m, beds CS13 and CS14, middle member, Sespe Formation. Most of the fossils collected by the CIT personnel at LACM(CIT) loc. 128 came from bed CS13; however, a few specimens were recovered from bed CS14. Taxa: *Sespedectes singularis; Dyseolemur pacificus; Protoreodon "pumilus"*; *Leptoreodon stocki* n. sp.; *Simimeryx hudsoni;* Artiodactyla gen. and sp. indet.

LACM(CIT) loc. 145. Lat. 34°17′51″N; Long. 118°47′20″W. West side, Brea Canyon, 84 m N 68°W of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 305 m, bed SS18, middle member, Sespe Formation. Photographs made during the original CIT investigations indicate the primary fossiliferous horizon referred to LACM(CIT) loc. 145 is bed SS18; however, a few specimens were recovered from the beds immediately above and below bed SS18. Taxa: Trionychidae gen. and sp. indet.; *Amynodontopsis bodei;* Artiodactyla gen. and sp indet.

LACM(CIT) loc. 146. Lat. 34°17′49″N; Long. 118°47′22″W. West side, Brea Canyon, 169 m S 72°W of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 293 m, bed SS16, middle member, Sespe Formation. This locality is in the lowest outcrop of white sandstone in the extreme southwest corner of the small canyon containing LACM(CIT) loc. 145. Taxa: *Sespedectes singularis; Chumashius balchi; Amynodontopsis bodei; Protylopus* sp.; *Leptoreodon stocki* n. sp.; Rodentia gen. and sp. indet.

LACM(CIT) loc. 147. Lat. 34°17′57″N; Long. 118°47′08″W. West side, Brea Canyon, 241 m N 49°E of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 317 m, bed SS21, middle member, Sespe Formation. This locality is in small exposure of red and green sandstone immediately below the CDLB fault. Taxa: *Protylopus pearsonensis;* Mammalia gen. and sp indet.

LACM(CIT) loc. 148. Lat. 34°17′52″N; Long. 118°47′04″W. West side, Brea Canyon, 372 m N 75°E of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 290 m, bed CS16, middle member, Sespe Formation. This locality is in the red claystone that overlies the conglomerate (SS16) that produces prominent oil seeps. Taxa: Rodentia gen. and sp. indet.; Mammalia gen. and sp. indet.

LACM(CIT) loc. 149. Lat. 34°18′03″N; Long. 118°47′11″W. West side, Brea Canyon, 395 m N 25.5°E of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 335 m, bed CS8?, middle member, Sespe Formation. This locality is located just above the CDLB fault in vertically uplifted strata that repeat strata below the fault. The exact stratigraphic position of LACM(CIT) loc. 149 can only be estimated. Based on the known vertical displacement of the fault, the bed that contains LACM(CIT) loc. 149 is probably equivalent to bed CS8 below the fault. Taxa: *Leptoreodon* sp. indet.; Mammalia gen. and sp. indet.

LACM(CIT) loc. 150. Lat. 34°17′53″N; Long. 118°47′26″W. Quarry near the head of of unnamed canyon between Brea and Alamos Canyons, 369 m N 81°W of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 290 m, bed CS20, middle member, Sespe Formation. This locality was destroyed by the Simi Valley Landfill operation. See the original CIT photographs of LACM(CIT) locs. 150, 150E, 150W, and 150.5, in the "Sespe Excavations 1933" on file at the LACM.

LACM(CIT) loc. 150E (east). Lat. 34°17′53″N; Long. 118°47′21″W. Approximately 201 m east of LACM(CIT) loc. 150 at east edge of unnamed canyon between Brea and Alamos Canyons, elevation approximately 320 m, bed CS20, middle member, Sespe Formation. LACM(CIT) loc. 150E is one of the few localities that has not yet been destroyed by the Simi Valley Landfill operation. See CIT photographs 577 and 588 in "Sespe Excavations 1933" on file at the LACM. Taxa: *Simimeryx hudsoni;* Rodentia gen. and sp. indet.

LACM(CIT) loc. 150W (west). Lat. 34°17′53″N; Long. 118°47′28″W. 92 m west of LACM(CIT) loc. 150 at the bottom of unnamed canyon between Brea and Alamos Canyons, approximate elevation 280 m, bed CS20, middle member, Sespe Formation. LACM(CIT) loc. 150W was destroyed by the Simi Valley Landfill operation.

LACM(CIT) loc. 150.5. Lat. 34°17′53″N; Long. 118°47′23″W. Geographically between LACM(CIT) locs. 150 and 150E in unnamed canyon between Brea and Alamos Canyons, approximate elevation 297 m, bed CS20, middle member, Sespe Formation. LACM(CIT) loc. 150.5 was destroyed by the Simi Valley Landfill operation. See CIT photograph 586 in the "Sespe Excavations 1933" on file at the LACM.

LACM(CIT) loc. 151. Lat. 34°17′37″N; Long. 118°46′52″W. East side, Brea Canyon, 767 m S 56°E of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 314 m, bed CS4, middle member, Sespe Formation. Taxa: *Protoreodon "pumilus"*; *Leptoreodon stocki* n. sp.

LACM(CIT) loc. 152. Lat. 34°17′49″N; Long. 118°46′16″W. East side, Brea Canyon, 1590 m S 87.5°E of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 330 m, bed CS5?, middle member, Sespe Formation. LACM(CIT) loc. 152 is located just above the CDLB fault in vertically uplifted strata that repeat strata below the fault. Based on similar lithologies, the stratigraphic position of LACM(CIT) loc. 152 is estimated to correlate with bed CS5 below the fault. Taxon: Mammalia gen. and sp. indet.

LACM(CIT) loc. 154. Lat. 34°17′29″N; Long. 118°47′26″W. West side, Brea Canyon, 762 m S 11°W of the most southerly Unocal oil well (CDLB #3) in Brea Canyon, elevation approximately 290 m, bed CS1, middle member, Sespe Formation. LACM(CIT) loc. 154 is in west side of Brea Canyon along the face of a cliff about 61 m above the canyon floor. The Conejo Volcanics, a Miocene intrusive unit, is exposed in this cliff face below LACM(CIT) loc. 154. Taxon: Mammalia gen. and sp. indet.

LACM(CIT) loc. 179. Lat. 34°17′38″N; Long. 118°48′11″W. 805 m east of Alamos Canyon in east fork of small tributary canyon, elevation approximately 302 m, bed CS15, middle member, Sespe Formation. Apparently, the original sample of fossils collected from LACM(CIT) loc. 179 was misplaced or lost during the transfer of the CIT collection to LACM. Taxon: *Protoreodon pacificus.* Also, Roeder (1982) collected a specimen, which he identified as Carnivora sp. indet., from this locality.

LACM(CIT) loc. 180. Lat. 34°18′20″N; Long. 118°44′21″W. East side, Dry Canyon, 4.67 km N 39.5°W of Santa Susana benchmark 961, elevation approximately 427 m, bed CS1?, middle member, Sespe Formation. Extensive fieldwork conducted for the present study indicates LACM(CIT) loc. 180 occurs very low in the middle member, just above the contact between the lower and middle members, and at about the stratigraphic level of bed CS1 in Brea Canyon. However, the exact stratigraphic position relative to the Brea Canyon section can only be estimated to be within 20 m of bed CS1. This locality yielded the majority of specimens assigned to the Tapo Canyon Local Fauna.

LACM(CIT) loc. 202. Lat. 34°17′32″N; Long. 118°47′38″W. Unnamed canyon between Brea and Alamos Canyons, elevation approximately 267 m, bed CS3, middle member, Sespe Formation. LACM(CIT) loc. 202 was destroyed by the Simi Valley Landfill operation. The precise stratigraphic positions of LACM(CIT) locs. 202 and 207 were determined by identifying still-existing exposures of the fossiliferous horizons from CIT photographs 653 and 654 of the original localities and by tracing individual beds from new exposures in the Simi Valley Landfill to exposures in Brea Canyon.

LACM(CIT) loc. 202E (east). Lat. 34°17′32″N; Long. 118°47′36″W. Just east of LACM(CIT) loc. 202 in unnamed canyon between Brea and Alamos Canyons, elevation approximately 275 m, bed CS3, middle member, Sespe Formation. LACM(CIT) loc. 202E was destroyed by the Simi Valley Landfill operation.

LACM(CIT) loc. 202W (west). Lat. 34°17′31″N; Long. 118°47′40″W. Just west of LACM(CIT) loc. 202 in unnamed canyon between Brea and Alamos Canyons, approximate elevation 259 m, bed CS3, middle member, Sespe Formation. LACM(CIT) loc. 202W was destroyed by the Simi Valley Landfill operation.

LACM(CIT) loc. 207. Lat. 34°17′33″N; Long. 118°47′40″W. Approximately 23 m below LACM(CIT) loc. 202 in unnamed canyon between Brea and Alamos Canyons, elevation approximately 244 m, bed CS2, middle member, Sespe Formation. LACM(CIT) loc. 207 was destroyed by the Simi Valley Landfill operation. See the CIT photographs 653 and 654 in the "Sespe Excavations 1933" on file at the LACM.

LACM(CIT) loc. 217. Lat. 34°18′44″N; Long. 118°44′59″W. West side, Dry Canyon, 5.15 km N 46°W of Santa Susana benchmark 961, stratigraphically just above LACM(CIT) loc. 180, elevation approximately 389 m, bed CS1?, middle member, Sespe Formation. Horizon estimated to be equivalent to one within 20 m of bed CS1 in Brea Canyon.

LACM(CIT) loc. 218. Lat. 34°17′44″N; Long. 118°48′00″W. Unnamed canyon between Brea and Alamos Canyons, 5.23 km S 60°W of Simi Valley benchmark 2231, elevation approximately 274 m, bed CS15, middle member, Sespe Formation. LACM(CIT) loc. 218 was destroyed by the Simi Valley Landfill operation.

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# Contributions in Science

## Systematics and Taxonomy of Island and Mainland Populations of Western Harvest Mice (*Reithrodontomys megalotis*) in Southern California

Paul W. Collins and Sarah B. George

Natural History Museum of Los Angeles County

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# SYSTEMATICS AND TAXONOMY OF ISLAND AND MAINLAND POPULATIONS OF WESTERN HARVEST MICE (*REITHRODONTOMYS MEGALOTIS*) IN SOUTHERN CALIFORNIA

PAUL W. COLLINS [1] AND SARAH B. GEORGE[2]

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**ABSTRACT.** Western harvest mice (*Reithrodontomys megalotis*) are classified into four subspecies in southern California. Samples from three California islands and 14 mainland localities from the Santa Ynez River to the Mexican border were examined for patterns of geographic variation, using morphometrics and allozymes. The sample from Santa Catalina Island is the most divergent, but even so, it can be considered to have colonized the island in the Holocene. Western harvest mice probably were introduced inadvertently to Santa Cruz and Santa Catalina islands by Indians, whereas the San Clemente populations probably were introduced by Europeans sometime in the last 100 years. On the mainland, patterns of variability do not exhibit geographic trends, nor do they correspond to presently accepted taxonomic classification. Based on these results, only one subspecies of western harvest mouse is recognized in coastal southern California, and *R. m. catalinae*, *R. m. limicola*, and *R. m. santacruzae* are relegated to synonymy under *R. m. longicaudus*.

## INTRODUCTION

The western harvest mouse (*Reithrodontomys megalotis*) has the widest geographic distribution of all North American harvest mice, ranging from southwestern Canada (British Columbia east to Saskatchewan) southward into southern Mexico (Oaxaca and Veracruz) and from California east into recently invaded Indiana (Ford, 1977; Hall, 1981; Webster and Jones, 1982). Probably because of this wide geographic distribution, *R. megalotis* exhibits a moderate amount of intraspecific variation in morphological characters, and at present 16 subspecies are recognized (Webster and Jones, 1982). Within this broad geographic range, western harvest mice have been found in a variety of habitats and elevations. These mice have been recorded from below sea level at Death Valley to above 3960 meters in southern Mexico (Webster and Jones, 1982). In California, western harvest mice tend to inhabit grassy and weedy habitats such as meadows, fence rows, fallow fields, overgrown pastures, coastal salt marshes, and borders of agricultural and riparian areas (Grinnell, 1933; Webster and Jones, 1982).

With the exception of Howell (1914), there has been no extensive effort made to study the systematics of this species over its entire range. Original descriptions for most of the subspecies were based on small samples composed of individuals of various ages, and the taxonomic legitimacy of some of these subspecies is in question. A few authors have conducted systematic studies over portions of the species' range. Fisler (1965) studied intraspecific variation in populations of *R. megalotis longicaudus* from the San Francisco Bay area. He found no appreciable sexual dimorphism and little local geographic variation in the six samples examined. Using only univariate statistical methods, Hoffmeister and Warnock (1955) reevaluated the taxonomic status of western harvest mice from the Midwest, whereas Jones and Mursaloglu (1961) studied geographic variation in western harvest mice on the central Great Plains. Hoffmeister (1986) examined and reported on the taxonomic status of western harvest mice from Arizona. In each of these studies, *R. megalotis* showed no significant sexual dimorphism and little intraspecific variation, and the authors relegated several previously described subspecies to synonymy with other forms. There has been no attempt to study geographic variation in western harvest mice using both allozymic and morpho-

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[1] Department of Vertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta Del Sol, Santa Barbara, California 93105.

[2] Section of Mammalogy, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

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metric data with univariate and multivariate statistical methods.

Hall (1981) and Webster and Jones (1982) currently recognize six subspecies of *R. megalotis* in California (*longicaudus, megalotis, distichlis, limicola, catalinae,* and *santacruzae*). West of the Sierra Nevada and Mojave Desert is a widespread, grassland form of harvest mouse, first described as *Reithrodon longicauda* by Baird (1857), but later relegated by Howell (1914) to subspecific status as *R. m. longicaudus* under the widespread species *R. megalotis.* North and east of the Sierra Nevada in the Great Basin and throughout much of the Colorado and Mojave deserts is the nominotypical subspecies. Von Bloeker (1932, 1937) described *R. m. limicola* from the salt marshes of southern California from Point Mugu, Ventura County, to Newport Bay, Orange County (Williams, 1986) and *R. m. distichlis* from the coastal salt marshes and sand hills from Elkhorn Slough to Seaside Lagoon in Monterey County. Both of these subspecies were characterized as having darker coloration than adjacent upland western harvest mice. Although Fisler (1965) found a similar tendency to dark pelage color in western harvest mice inhabiting salt marshes in the San Francisco Bay area, he did not feel that this character was sufficient to warrant subspecific classification for those populations. Pearson (1951) could not find differences between *R. m. distichlis* and *R. m. longicaudus,* and in preliminary analyses, we could find no significant morphological or allozymic evidence to support the continued recognition of *R. m. limicola* in southern California. Therefore, the taxonomic status of populations of western harvest mice in California is in need of review.

Western harvest mice have been found on three of the California islands: San Clemente, Santa Catalina, and Santa Cruz. According to von Bloeker (1967), the harvest mice on San Clemente Island were introduced from populations of *R. m. longicaudus* from the adjacent mainland, but until now, the taxonomic affinities of the San Clemente Island population have not been examined thoroughly. The Santa Catalina Island form was originally described as *Rhithrodontomys* (*sic*) *catalinae* (Elliot, 1904) but was later relegated to subspecific status as *R. m. catalinae* (Grinnell, 1913; Hooper, 1952). Harvest mice were discovered on Santa Cruz Island in 1948 and were described by Pearson (1951) as *R. m. santacruzae.* Both of the island subspecies can be differentiated from adjacent mainland taxa on the basis of their larger size (Elliot, 1904; Pearson, 1951), but they were described on the basis of only a few specimens.

Few studies have been published on genic variability within *R. megalotis.* Arnold *et al.* (1983) examined 20 presumptive loci in a sample of 13 individuals from Arkansas, California, Kansas, New Mexico, and Tlaxcala; only three loci were variable. Nelson *et al.* (1984) examined 30 isozymes in a sample of seven individuals from California, Kansas, and Texas and, again, found only three loci to be variable. No work has been published examining genic variability within or among large samples of western harvest mice.

Our objectives are to (1) reevaluate the taxonomic status of coastal salt marsh and island populations of *R. megalotis* in southern California using both allozymic (electrophoretic) and morphometric characters; (2) determine whether the patterns of morphologic and genic variation are concordant in these populations; (3) develop explanations for the patterns of differentiation observed by examining the possible underlying causes; (4) determine the extent that subspecies of harvest mice in southern California represent the kind of evolutionary unit espoused by present-day systematists (*e.g.,* Barrowclough, 1982; Monroe, 1982; Thorpe, 1987); (5) examine the possibility that one or more of the island populations were purposefully or accidentally introduced by humans; and (6) test the hypothesis that populations of *R. megalotis* from coastal salt marshes in southern California are contiguous with, and have diverged little from, adjacent upland populations.

## METHODS

### ALLOZYMIC ANALYSES

For the allozyme analyses, 208 individuals were examined. Specimens were assigned to 15 samples (Fig. 1); sample sizes and localities are listed in the Appendix. Heart, liver, and kidneys were taken from each specimen at death and stored at −70°C until processed; in a few cases, tissues were removed from animals frozen at −5°C for several weeks (George, 1988). Tissue preparation (heart and kidneys were processed together), horizontal starch-gel electrophoresis, and biochemical staining procedures were modified from techniques described by Selander *et al.* (1971). Wherever possible, NAD-dependent glucose-6-phosphate dehydrogenase (G-6-PDH) was substituted for NADP-dependent G-6-PDH as a cost-saving measure (Buth and Murphy, 1980). Gels were prepared from Connaught starch. Buffer systems were those of Selander *et al.* (1971), as follows: I—continuous tris-citrate I (3.5 hr, 150 V, heart and kidneys), II—continuous tris-citrate II (5 hr, 130 V, liver), III—phosphate (4 hr, 130 V, liver). Thirty presumptive loci were examined (acronyms and buffer systems in parentheses): albumin (AB; I), hemoglobin (HB; I), lactate dehydrogenase (LDH-1, LDH-2; I), glucose-phosphate isomerase (GPI; I), isocitrate dehydrogenase (ICD; I), peptidase A (glycyl-leucine, Pep-A; I), peptidase B (leucyl-glycyl-glycine, Pep-B; I), peptidase D (phenylalanyl-proline, Pep-D; I), malic enzyme (ME; I), malate dehydrogenase (MDH-1, MDH-2; I), sorbitol dehydrogenase (SDH; I), superoxide dismutase (SOD; II), $\alpha$-glycerophosphate dehydrogenase ($\alpha$-GPD; II), alcohol dehydrogenase (ADH; II), glutamate oxaloacetate dehydrogenase (Got-1, Got-2; II), esterase (Est-1, Est-2; II), purine nucleoside phosphorylase (NP; III), phosphoglucomutase (PGM; I), adenylate kinase (AdK; I), creatine kinase (Ck-1, Ck-2; III), glucose-6-phosphate dehydrogenase (G6PDH; I), 6-phosphogluconate dehydrogenase (6-PGD; I), diaphorase (Dia; III), adenosine deaminase (ADA; III), leucine amino peptidase (LAP; II). Alleles for each locus were designated alphabetically, beginning with

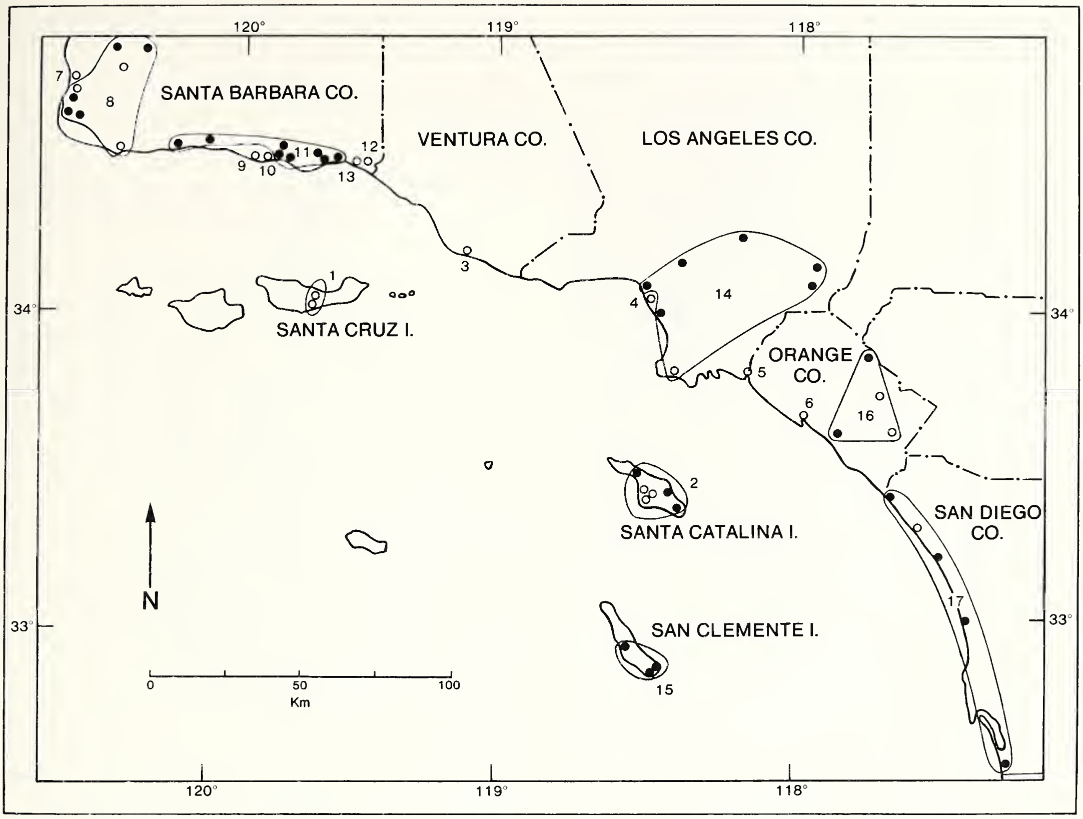

**Figure 1.** Map of sample localities. Closed dots denote localities where individuals were used only in morphometric analyses; open dots mark localities included in both morphometric and allozymic analyses. Numbers refer to the following samples: (1) SCRUZI, (2) SCATI, (3) PTMUGU, (4) DELREY, (5) ANAHEM, (6) NEWPRT, (7) STYNEZ, (8) NSBARB, (9) DEVERO, (10) GOLETA, (11) SSBARB, (12) CARPUP, (13) CARPIN, (14) LACOUP, (15) SCLEMI, (16) ORANGE, (17) SDIEGO. Acronyms are defined and localities are listed in the Appendix.

the most anodal position. Allozymes that migrated cathodally were designated with a negative sign. Side-by-side comparisons of mobilities of allozymes on the same gel were used for comparison of alleles.

Allelic frequencies, estimates of mean heterozygosity (*H*), and percent loci polymorphic (*P*) were calculated for each species. Matrices of Nei's (1972) identity and Rogers' (1972) similarity and distance were generated from the genic data. Cluster analysis of Nei's distance matrix was performed with the unweighted pair-group method using arithmetic means (UPGMA) of BIOSYS-1 (Swofford and Selander, 1981). The distance-Wagner procedure (DISWAG of BIOSYS-1 with addition criteria III and rooted at the midpoint) was employed with Rogers' distance matrix. *F*-statistics were calculated to apportion the total genetic variation into inbreeding coefficients within populations ($F_{IS}$) and within the total population ($F_{IT}$) and into allelic variance among populations ($F_{ST}$), using the FSTAT step of BIOSYS-1 (Nei, 1977; Swofford and Selander, 1981).

## MORPHOMETRIC ANALYSES

A total of 457 western harvest mice from 14 mainland and three island samples in southern California (Fig. 1) were examined for morphometric analyses. The samples are similar to those included in the allozymic study, with the exception of samples 11 (southern Santa Barbara County) and 15 (San Clemente Island) for which we had no tissues. Sample sizes and localities for specimens used in the final data set are listed in the Appendix. Fourteen cranial measurements were taken from each specimen (Fig. 2), following the methods described in Hooper (1952) and Fisler (1965) unless otherwise indicated: greatest length of skull (GL), breadth of braincase (BB), length of braincase (LBC, measured from the leading edge of the shallow notch on the superior orbital border of the zygomatic arch to the occipital condyle), zygomatic breadth (ZB), breadth of rostrum (BR), depth of braincase (DBC, measured by resting the calipers on the basisphenoid and basioccipital sutures and measuring to the dorsal surface of the cranium), intermeatus width (IMW, the least distance between the bullae measured at the basioccipital suture), length of rostrum (LR, measured from the leading edge of the shallow notch on the superior orbital border of the zygomatic arch to the tip of the nasals), length of nasals (LN), length of incisive foramen (LIF), length of molar toothrow (AL), interorbital breadth (IB), length of palate (LP, measured from the posterior edge of the alveoli of the incisors to the mesopterygoid fossa), breadth of zygomatic plate (BZP). The first six measurements were taken with dial calipers to the nearest 0.01 mm, whereas the remaining eight measurements were taken with an ocular micrometer to the nearest 0.1 mm. Specimens lack-

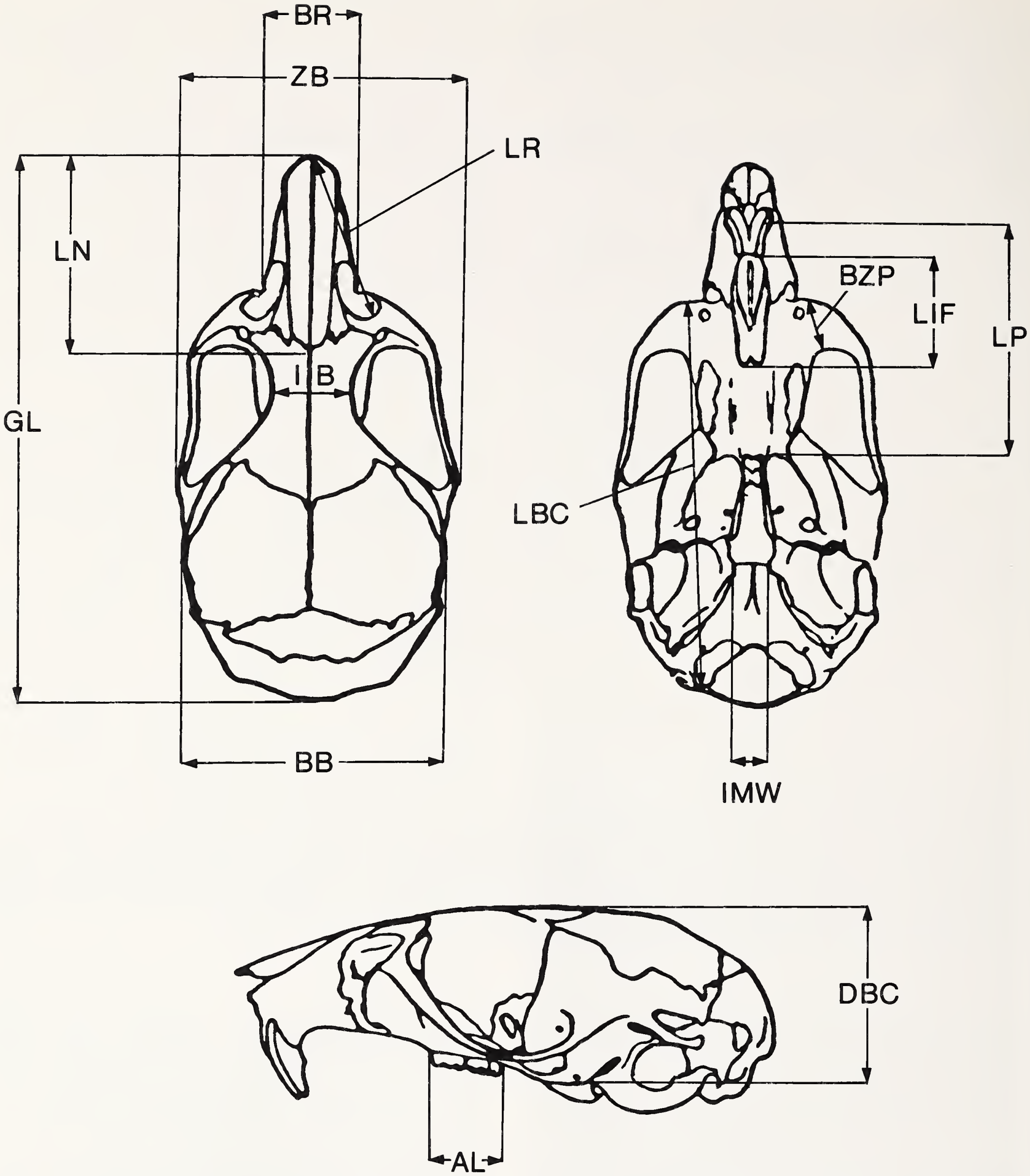

**Figure 2.** Fourteen cranial measurements used in this study; acronyms are defined and described in the Methods section.

ing one or more measurements were excluded from the analyses.

Specimens were assigned to one of six age categories based on wear of the upper molars. The categories correspond to the age classes described by Fisler (1965) except where noted as follows: juvenile (class 1 of Fisler [1965]), subadult (class 2), young adult (class 3), adult (class 4; and confluent dentine canal connecting the protocone, paracone, and metacone [Hoffmeister, 1986]), middle-aged adult (class 5), old adult (class 6).

Using BIOSTAT I, univariate statistics were calculated for all samples and variables; tests of normality, Student-Newman-Keuls (SNK) multiple range tests, and analyses of variance were obtained using BIOSTAT II (Pimentel and Smith, 1986a, b). To examine the extent of secondary sexual variation in *R. megalotis,* the 14 cranial measurements for males and females were compared from one island sample (Santa Catalina, sample 2) and three mainland samples (Santa Barbara County upland combined, samples 8 and 11; Goleta and Devereux sloughs combined, samples 9 and 10; and Point Mugu, sample 3), using *t*-tests (BIOSTAT I; Pimentel and Smith, 1986a). Ontogenetic variation was studied by comparing means of the 14 cranial variables among age classes for the Santa Catalina Island sample and the northern and southern Santa Barbara County upland samples combined. Methods used were the SNK multiple range tests to determine the maximal nonsignificant subsets and *F*-tests (BIOSTAT II; Pimentel and Smith, 1986b).

Based on results of the studies of secondary sexual and ontogenetic variation, we elected to combine sexes and age classes 2–6 for all samples (see Results section). Tests of normality indicated that three variables (BB, IB, and BZP) exhibit significant departures from normality, being negatively skewed and highly leptokurtotic. These variables were excluded from the multivariate analyses. Despite slight leptokurtosis, BR and LR were included. Multigroup discriminant function analysis was performed using BIOSTAT II (Pimentel and Smith, 1986b).

## RESULTS

### ALLOZYMIC VARIATION

Of the 30 loci examined, 10 were fixed for a single allele across the 15 samples, and 20 were polymorphic in at least one sample (Table 1). Unique alleles were detected in nine populations: SCATI (Pep-$A^A$, Ck-$2^{-B}$), DELREY ($\alpha$-$GPD^C$), ANAHEM ($ME^B$), STYNEZ (Pep-$A^B$, 6-$PGD^C$), GOLETA ($G6PDH^A$), DEVERO ($GPI^{-A}$, $DIA^A$), CARPIN (Pep-$A^D$, $NP^A$), CARPUP (6-$PGD^D$), SDIEGO (6-$PGD^B$). With the exception of Ck-$2^{-B}$ in population SCATI, the unique alleles exist at low frequencies.

Geographic patterns of variation may be discerned for a few loci. For LDH-2, allele A appears at low levels in southern populations only (ANAHEM, LACOUP, SDIEGO). Allozyme B at ADH appears in the three southernmost populations (NEWPRT, ORANGE, SDIEGO) but also shows up at PTMUGU; a similar pattern is seen for allozyme B at Got-1, which also is seen in another southern population (LACOUP). Interestingly, allele A at ADA is found in both island samples and in every population from PTMUGU south, with the exception of sample ORANGE. The populations assigned to *R. m. limicola* do not differ appreciably from populations assigned to *R. m. longicaudus* when patterns of geographic variation in single loci are examined. There are no fixed differences at any loci, and with two exceptions, the common allele for each locus is the same for all populations. For the sample from Santa Catalina Island, allele B (rather than C) is in the highest frequency at Pep-D, and allele A (rather than B) is in the highest frequency at ADA.

Mean heterozygosity (*H*) within populations ranges from 0.03 to 0.08 (Table 2) (mean = 0.04 across all samples). Using the 0.95 criterion (*i.e.*, excluding loci for which the common allele is at a frequency above 0.95), polymorphism within populations varies from 6.7 to 26.7%, whereas using the 0.99 criterion, polymorphism varies from 10 to 26.7%. The latter values are identical to values calculated using no criterion at all (*i.e.*, including all polymorphic loci, regardless of allelic frequency). Across all samples, polymorphism is 13.3% using the 0.95 criterion, 36.7% using the 0.99 criterion, and 66.7% using no criterion at all.

*F*-statistics averaged across all loci and all populations sampled were $F_{IS} = 0.245$, $F_{IT} = 0.307$, and $F_{ST} = 0.081$. In other words, only 8.1% of the total genetic variation found in these populations may be ascribed to among population variation. The average inbreeding coefficient within samples is 0.245, whereas the inbreeding coefficient among samples is 0.307.

The UPGMA phenogram (Fig. 3) of Nei's distance matrix shows all populations clustering below the 2.3% level. The cophenetic correlation coefficient of the phenogram is 0.917, indicating that little distortion of the distance values was necessary to construct the tree. UPGMA clustering of the identity matrix yielded a tree with identical topology and a cophenetic correlation coefficient of 0.952. The first population to diverge is that from Santa Catalina Island; the second is that from Newport Bay, at the 1.4% level. The remaining populations cluster at or below the 0.7% distance. No recognizable patterns that correspond to geography or taxonomic subdivisions can be discerned from the clustered samples. There are no obvious north–south clines, and although three of the four populations attributed to the marshland subspecies, *R. m. limicola* (DELREY, ANAHEM, PTMUGU), are together, they are clustered with the sample from Santa Cruz Island. The fourth population classified as *R. m. limicola* (NEWPRT) is the second-most divergent sample examined.

The distance-Wagner tree (Fig. 4), rooted at the midpoint, has a cophenetic correlation coefficient of 0.904 and shows a pattern of clustering similar to that seen in both UPGMA phenograms. There are neither north–south nor wetland–upland patterns of clustering. Samples from Santa Catalina Island and Newport Bay have the greatest branch length. This may be explained by the sample from Newport Bay having the highest rate of heterozygosity (0.08) and the sample from Santa Catalina Island having unusual allele frequencies at two loci, Pep-D and ADA (Table 1).

### MORPHOLOGIC VARIATION

Summary statistics (mean, range, standard deviation, and coefficient of variation), results of Student-Newman-Keuls multiple range tests, and analysis of variance for each of the 11 cranial characters are shown in Table 2. Analysis of variance revealed highly significant differences ($P < 0.001$) among samples for each character.

#### Nongeographic Variation

**Sexual Variation.** Males average larger than females in each of the four samples tested for only four measurements (GL, DBC, IW, LIF), whereas females are larger in four measurements (LR, AL, BR, BZP). These differences are not statistically significant ($P > 0.05$). The remaining six measurements show no consistent pattern in sexual dimorphism across the four samples. Only IW, BR, and BZP show statistically significant ($P < 0.0001$) differences between the sexes, but the dimorphism is significant for each measurement in only one of the four samples (IW in sample 8/11, BR in sample 9/10, BZP in sample 3). Because none of the 14

Table 1. Electromorphs, mean heterozygosity (*H*), percent polymorphism (P) (95% and 99% criteria), and *F*-statistics for 20 polymorphic loci scored across 15 populations of ***Reithrodontomys megalotis*** in southern California. Allelic designations are described in text. Where a locus is polymorphic within a population, allelic frequencies are given in parentheses.

| Sample | n | LDH-2 | GPI | ICD | Pep-D | Pep-B | Pep-A | ME |
|---|---|---|---|---|---|---|---|---|
| SCRUZI | 20 | B | −B | C | C | B | C | A |
| SCATI | 15 | B | −B | A (0.03)<br>C (0.97) | B (0.67)<br>C (0.33) | B | A (0.07)*<br>C (0.93) | A |
| PTMUGU | 20 | B | −B | C (0.97)<br>D (0.03) | A (0.05)†<br>B (0.25)<br>C (0.70) | B | C | A |
| DELREY | 15 | B | −B | C | B (0.13)<br>C (0.70) | B | C | A |
| ANAHEM | 15 | A (0.07)<br>B (0.93) | −B | C | A (0.10)†<br>B (0.13)<br>C (0.77) | A (0.13)<br>B (0.87) | C | A (0.93)*<br>B (0.03) |
| NEWPRT | 11 | B | −B | C | A (0.09)<br>B (0.41)<br>C (0.50) | B | C | A |
| STYNEZ | 18 | B | −B | B (0.03)<br>C (0.97) | B (0.28)<br>C (0.72) | B | B (0.03)<br>C (0.97) | A |
| NSBARB | 14 | B | −B | C | C | B | C | A |
| DEVERO | 13 | B | −A (0.04)<br>−B (0.96) | C | B (0.12)<br>C (0.88) | A (0.04)<br>B (0.96) | C | A |
| GOLETA | 13 | B | −B | A (0.04)*<br>B (0.08)<br>C (0.88) | A (0.08)†<br>B (0.31)<br>C (0.61) | A (0.04)<br>B (0.96) | C | A |
| CARPUP | 12 | B | −B | C | B (0.38)<br>C (0.62) | B | C | A |
| CARPIN | 14 | B | −B | C | B (0.07)*<br>C (0.93) | B | C (0.96)<br>D (0.04) | A |
| LACOUP | 11 | A (0.09)*<br>B (0.91) | −B | C | B (0.18)<br>B (0.82) | B | C | A |
| ORANGE | 10 | B | −B | C | B (0.05)<br>C (0.95) | B | C | A |
| SDIEGO | 7 | A (0.07)<br>B (0.93) | −B | C (0.93)<br>D (0.07) | C | B | C | A |
| $F_{IS}$ | | 0.346 | −0.040 | 0.231 | −0.088 | −0.109 | 0.487 | 1.000 |
| $F_{IT}$ | | 0.388 | −0.003 | 0.273 | 0.132 | −0.014 | 0.509 | 1.000 |
| $F_{ST}$ | | 0.063 | 0.036 | 0.054 | 0.202 | 0.086 | 0.044 | 0.063 |

* Allelic frequencies do not conform with expectations from Hardy-Weinberg equilibrium.

† Pooling rare alleles causes frequencies to conform to Hardy-Weinberg expectations.

cranial variables show statistically significant ($P < 0.05$) secondary sexual variation across all four of the samples tested, and all previous studies have shown that *R. megalotis* does not exhibit significant sexual dimorphism (Hooper, 1952; Jones and Mursaloglu, 1961; Fisler, 1965; Hoffmeister, 1986), the sexes were pooled with individuals of unknown sex.

***Intraspecific Ontogenetic Variation.*** Seven of the 14 cranial characters exhibit significant ($P \leq 0.05$) differences among the character means of the five age classes tested (Table 3). Five of the seven measurements previously have been shown to vary ontogenetically in western harvest mice (LR, LN, BR, LP, and ZB); four of these are measurements of the rostral area (Hooper, 1952; Fisler, 1965). SNK mul-

Table 1. Continued.

| Sample | n | SDH | α-GPD | ADH | Got-1 | Got-2 | NP | PGM |
|---|---|---|---|---|---|---|---|---|
| SCRUZI | 20 | −A | A (0.97)<br>B (0.03) | −A | A | B | B | A |
| SCATI | 15 | −A (0.93)*<br>−B (0.07) | A | −A | A | B | B | A |
| PTMUGU | 20 | −A | A (0.87)<br>B (0.13) | −A (0.95)<br>−B (0.05) | A (0.95)<br>B (0.05) | B | B | A (0.97)<br>B (0.03) |
| DELREY | 15 | −A | A (0.97)<br>C (0.03) | −A | A | B | A (0.07)<br>B (0.93) | A |
| ANAHEM | 15 | −A | A | −A | A | B (0.97)<br>C (0.03) | B (0.97)<br>C (0.03) | A |
| NEWPRT | 11 | −A | A | −A (0.96)<br>−B (0.04) | A (0.96)<br>B (0.04) | A (0.09)<br>B (0.64)<br>C (0.27) | B (0.91)<br>C (0.09) | A |
| STYNEZ | 18 | −A (0.97)<br>−B (0.03) | A | −A | A | B (0.97)<br>C (0.03) | B | A (0.97)<br>B (0.03) |
| NSBARB | 14 | −A | A | −A | A | B (0.86)<br>C (0.14) | B | A |
| DEVERO | 13 | −A | A | −A | A | B (0.92)<br>C (0.08) | A (0.08)*<br>B (0.92) | A |
| GOLETA | 13 | −A | A | −A | A | B (0.96)<br>C (0.04) | B (0.96)<br>C (0.04) | A |
| CARPUP | 12 | −A | A | −A | A | B | B | A |
| CARPIN | 14 | −A | A (0.89)<br>B (0.11) | −A | A | B (0.96)<br>C (0.04) | B | A (0.96)<br>C (0.04) |
| LACOUP | 11 | −A | A | −A | A (0.96)<br>B (0.04) | B (0.91)<br>C (0.09) | B (0.96)<br>C (0.04) | A |
| ORANGE | 10 | −A | A | −A (0.90)*<br>−B (0.10) | A (0.95)<br>B (0.05) | B | B | A |
| SDIEGO | 7 | −A | A | −A (0.93)<br>−B (0.07) | A (0.93)<br>B (0.07) | A (0.07)<br>B (0.93) | B | A |
| $F_{IS}$ | | 0.689 | −0.110 | 0.325 | −0.057 | 0.014 | 0.163 | −0.031 |
| $F_{IT}$ | | 0.704 | −0.018 | 0.363 | −0.018 | 0.141 | 0.205 | −0.004 |
| $F_{ST}$ | | 0.049 | 0.083 | 0.057 | 0.037 | 0.128 | 0.049 | 0.026 |

tiple-range tests record no consistent pattern of ontogenetic variation (Table 3). Although three variables (GL, LR, and ZB) exhibit significant variation in both samples tested, only ZB shows a similar pattern in both cases. Classes 2, 3, and 4 are statistically similar for two variables (LN and ZB) in the Santa Catalina Island sample and for five variables (GL, DBC, LR, ZB, and LP) in the Santa Barbara County group (Table 3). In the former sample, BR is the only character for which age class 2 (subadult) was significantly different from all other age classes, and LR is the only character in which age classes 4 (adult) and 5 (including middle-aged and old adults) were significantly different from each other and from age classes 2 and 3. As there was no consistent pattern of ontogenetic variation ev-

Table 1. Continued.

| Sample | n | 6-PGD | G6PDH | Dia | ADA | Ck-2 | Est-2 | *H* | P (95%) | P (99%) |
|---|---|---|---|---|---|---|---|---|---|---|
| SCRUZI | 20 | C | B | B | A (0.20)*<br>B (0.80) | −A | B (0.07)*<br>C (0.93) | 0.003 | 6.7 | 10.0 |
| SCATI | 15 | C | B | B | A (0.60)<br>B (0.40) | −A (0.87)*<br>−B (0.13) | B (0.10)<br>C (0.90) | 0.044 | 20.0 | 23.3 |
| PTMUGU | 20 | C | B | B | A (0.05)<br>B (0.95) | −A | B (0.05)<br>C (0.95) | 0.038 | 20.0 | 26.7 |
| DELREY | 15 | C | B | B | A (0.13)<br>B (0.87) | −A | B (0.10)<br>C (0.90) | 0.031 | 13.3 | 16.7 |
| ANAHEM | 15 | C | B | B | A (0.20)*<br>B (0.80) | −A | B (0.10)<br>C (0.90) | 0.038 | 20.0 | 26.7 |
| NEWPRT | 11 | C | B | B | A (0.27)<br>B (0.23)<br>C (0.41)<br>D (0.32) | −A | A (0.04)<br>B (0.23)<br>C (0.41)<br>D (0.32) | 0.076 | 16.7 | 23.3 |
| STYNEZ | 18 | A (0.06)<br>C (0.94) | B | B | B (0.89)<br>D (0.11) | −A | B (0.33)*<br>C (0.67) | 0.054 | 13.3 | 30.0 |
| NSBARB | 14 | C | B | B | B (0.93)<br>D (0.07) | −A | B (0.39)*<br>C (0.61) | 0.036 | 10.0 | 10.0 |
| DEVERO | 13 | C | B | A (0.08)*<br>B (0.92) | B | −A | B (0.54)<br>C (0.46) | 0.044 | 16.7 | 23.3 |
| GOLETA | 13 | C | A (0.04)<br>B (0.96) | B | B (0.81)<br>C (0.19) | −A | B (0.27)<br>C (0.73) | 0.049 | 13.3 | 26.7 |
| CARPUP | 12 | C (0.96)<br>D (0.04) | B | B | B | −A | A (0.04)<br>B (0.25)<br>C (0.67)<br>D (0.04) | 0.039 | 6.7 | 10.0 |
| CARPIN | 14 | C | B | B | B (0.96)<br>C (0.04) | −A | A (0.04)<br>B (0.21)<br>C (0.68)<br>D (0.07) | 0.040 | 10.0 | 23.3 |
| LACOUP | 11 | C | B | B | A (0.04)<br>B (0.96) | −A | A (0.04)<br>B (0.50)<br>C (0.46) | 0.036 | 13.3 | 23.3 |
| ORANGE | 10 | C | B | B | B | −A | B (0.30)<br>C (0.65)<br>D (0.05) | 0.027 | 13.3 | 13.3 |
| SDIEGO | 7 | B (0.07)<br>C (0.93) | B | B | A (0.21)<br>B (0.79) | −A | B (0.50)<br>C (0.50) | 0.057 | 26.7 | 26.7 |
| $F_{IS}$ | | −0.063 | −0.040 | 1.000 | 0.275 | 1.000 | −0.087 | | | |
| $F_{IT}$ | | −0.008 | −0.003 | 1.000 | 0.424 | 1.000 | 0.069 | | | |
| $F_{ST}$ | | 0.052 | 0.036 | 0.072 | 0.206 | 0.126 | 0.143 | | | |

ident, we regard specimens classed age 2 or above as adults and specimens classed ages 1 or 0 as juveniles. Subadults and adults were pooled for all subsequent analyses.

Results of our examination of ontogenetic variation in *R. megalotis* generally agree with those of Hooper (1952), Fisler (1965), and Hoffmeister (1986). Older mice, particularly those in age classes 5 and 6, are larger on average than animals classed ages 2–4 (Table 3). Hooper (1952) noted that senile individuals (age class 6) are unsatisfactory for use in taxonomic treatments because their skulls are often misshapen and their teeth are excessively eroded. Fisler (1965), therefore, decided to eliminate both old adults and juveniles from his study of geographic variation of harvest mice in the San

Table 2. Geographic variation in 11 cranial measurements (millimeters) for 17 populations of *Reithrodontomys megalotis* from southern California. Population samples and measurements are explained in the Appendix and Methods section. Vertical lines alongside each geographic sample indicate statistically homogeneous subsets derived from a Student-Newman-Keuls multiple range test. All *F*-statistics are significant ($P < 0.0001$).

| Sample no. | n | Mean | Range | SD | CV |
|---|---|---|---|---|---|
| Greatest length of skull (GL) ($F = 16.38$) | | | | | |
| 8 | 25 | 19.97 | 18.62–21.10 | 0.61 | 3.04 |
| 9 | 21 | 20.05 | 19.19–20.76 | 0.41 | 2.06 |
| 4 | 11 | 20.10 | 19.27–20.64 | 0.43 | 2.14 |
| 16 | 20 | 20.14 | 18.50–21.01 | 0.68 | 3.40 |
| 10 | 24 | 20.16 | 19.25–21.39 | 0.57 | 2.81 |
| 12 | 28 | 20.17 | 19.25–21.32 | 0.49 | 2.42 |
| 3 | 50 | 20.17 | 18.98–21.45 | 0.53 | 2.62 |
| 6 | 12 | 20.17 | 18.47–21.25 | 0.86 | 4.25 |
| 15 | 14 | 20.23 | 19.29–21.46 | 0.68 | 3.34 |
| 17 | 23 | 20.24 | 19.31–21.55 | 0.54 | 2.66 |
| 11 | 29 | 20.31 | 18.70–21.52 | 0.70 | 3.47 |
| 14 | 18 | 20.35 | 19.61–21.29 | 0.43 | 2.13 |
| 5 | 17 | 20.40 | 18.90–21.79 | 0.79 | 3.86 |
| 13 | 24 | 20.44 | 19.47–21.22 | 0.46 | 2.25 |
| 7 | 19 | 20.52 | 19.78–21.41 | 0.48 | 2.34 |
| 2 | 94 | 21.20 | 18.56–22.78 | 0.74 | 3.50 |
| 1 | 28 | 21.39 | 19.44–22.25 | 0.62 | 2.89 |
| Depth of braincase (DBC) ($F = 6.81$) | | | | | |
| 8 | 25 | 6.43 | 6.06–6.77 | 0.18 | 2.86 |
| 13 | 24 | 6.47 | 5.84–7.01 | 0.27 | 4.19 |
| 10 | 24 | 6.48 | 6.15–7.00 | 0.22 | 3.32 |
| 14 | 18 | 6.51 | 6.04–7.03 | 0.24 | 3.64 |
| 17 | 23 | 6.51 | 6.02–6.81 | 0.17 | 2.55 |
| 16 | 20 | 6.52 | 6.25–6.93 | 0.18 | 2.75 |
| 6 | 12 | 6.52 | 6.21–6.86 | 0.18 | 2.76 |
| 12 | 28 | 6.52 | 6.20–6.86 | 0.18 | 2.77 |
| 15 | 14 | 6.53 | 5.99–6.86 | 0.26 | 4.03 |
| 11 | 29 | 6.54 | 6.19–6.98 | 0.21 | 3.17 |
| 9 | 21 | 6.55 | 6.31–6.89 | 0.18 | 2.75 |
| 4 | 11 | 6.58 | 6.32–6.91 | 0.21 | 3.22 |
| 5 | 17 | 6.60 | 6.29–6.98 | 0.18 | 2.77 |
| 7 | 19 | 6.61 | 6.32–6.86 | 0.16 | 2.43 |
| 3 | 50 | 6.61 | 6.20–7.21 | 0.20 | 2.98 |
| 1 | 28 | 6.65 | 6.22–7.00 | 0.20 | 3.04 |
| 2 | 94 | 6.75 | 6.22–7.31 | 0.20 | 3.00 |
| Intermeatus width (IW) ($F = 2.77$) | | | | | |
| 10 | 24 | 2.28 | 2.10–2.50 | 0.12 | 5.06 |
| 9 | 21 | 2.30 | 2.10–2.70 | 0.12 | 5.40 |
| 4 | 11 | 2.31 | 2.10–2.50 | 0.15 | 6.26 |
| 8 | 25 | 2.32 | 2.00–2.70 | 0.17 | 7.34 |
| 15 | 14 | 2.33 | 2.10–2.60 | 0.13 | 5.69 |
| 11 | 29 | 2.37 | 2.10–2.80 | 0.20 | 8.60 |
| 13 | 24 | 2.37 | 2.20–2.60 | 0.13 | 5.30 |
| 17 | 23 | 2.38 | 2.20–2.80 | 0.14 | 5.94 |
| 7 | 19 | 2.38 | 2.00–3.00 | 0.22 | 9.30 |
| 12 | 28 | 2.40 | 2.00–2.70 | 0.15 | 6.27 |
| 16 | 20 | 2.40 | 1.90–3.00 | 0.23 | 9.65 |
| 3 | 50 | 2.40 | 1.51–2.90 | 0.23 | 9.57 |
| 14 | 18 | 2.41 | 2.20–2.80 | 0.16 | 6.61 |
| 1 | 28 | 2.43 | 1.54–2.90 | 0.24 | 9.90 |
| 2 | 94 | 2.44 | 1.10–2.90 | 0.24 | 9.72 |
| 6 | 12 | 2.47 | 2.30–2.60 | 0.10 | 3.99 |
| 5 | 17 | 2.57 | 2.20–2.80 | 0.17 | 6.42 |

Table 2. Continued.

| Sample no. | n | Mean | Range | SD | CV |
|---|---|---|---|---|---|
| Length of rostrum (LR) ($F = 15.41$) | | | | | |
| 15 | 14 | 6.24 | 5.60–6.80 | 0.32 | 5.10 |
| 10 | 24 | 6.26 | 5.60–6.70 | 0.25 | 3.91 |
| 4 | 11 | 6.27 | 5.90–6.80 | 0.28 | 4.46 |
| 16 | 20 | 6.28 | 5.50–6.90 | 0.37 | 5.86 |
| 3 | 50 | 6.30 | 5.50–6.90 | 0.33 | 5.27 |
| 9 | 21 | 6.31 | 5.70–6.70 | 0.23 | 3.68 |
| 8 | 25 | 6.34 | 5.80–6.90 | 0.28 | 4.39 |
| 13 | 24 | 6.38 | 5.80–6.80 | 0.23 | 3.60 |
| 6 | 12 | 6.40 | 5.70–7.10 | 0.44 | 6.79 |
| 5 | 17 | 6.41 | 5.70–7.10 | 0.39 | 6.01 |
| 12 | 28 | 6.41 | 5.60–7.20 | 0.37 | 5.74 |
| 11 | 29 | 6.42 | 5.60–7.10 | 0.40 | 6.16 |
| 7 | 19 | 6.47 | 5.80–7.10 | 0.30 | 4.67 |
| 17 | 23 | 6.47 | 6.10–7.30 | 0.32 | 4.94 |
| 14 | 18 | 6.74 | 6.20–7.50 | 0.33 | 4.88 |
| 2 | 94 | 6.86 | 5.50–7.60 | 0.39 | 5.68 |
| 1 | 28 | 7.04 | 5.60–7.80 | 0.43 | 6.05 |
| Length of braincase (LBC) ($F = 20.07$) | | | | | |
| 9 | 21 | 13.80 | 13.28–14.16 | 0.26 | 1.88 |
| 16 | 20 | 13.85 | 12.86–14.54 | 0.44 | 3.19 |
| 6 | 12 | 13.89 | 12.89–14.66 | 0.54 | 3.89 |
| 17 | 23 | 13.90 | 13.25–14.73 | 0.37 | 2.63 |
| 10 | 24 | 13.92 | 13.28–14.59 | 0.40 | 2.91 |
| 11 | 29 | 14.03 | 12.92–14.84 | 0.46 | 3.26 |
| 5 | 17 | 14.10 | 13.33–15.09 | 0.48 | 3.37 |
| 8 | 25 | 14.13 | 12.76–15.05 | 0.62 | 4.41 |
| 7 | 19 | 14.23 | 13.62–15.19 | 0.40 | 2.82 |
| 3 | 50 | 14.44 | 13.37–15.69 | 0.53 | 3.64 |
| 14 | 18 | 14.48 | 13.95–15.16 | 0.36 | 2.47 |
| 13 | 24 | 14.49 | 13.50–15.35 | 0.40 | 2.73 |
| 4 | 11 | 14.53 | 13.30–15.19 | 0.61 | 4.17 |
| 12 | 28 | 14.63 | 13.69–15.23 | 0.37 | 2.56 |
| 1 | 28 | 14.88 | 14.04–15.44 | 0.37 | 2.46 |
| 15 | 14 | 14.90 | 14.48–15.79 | 0.37 | 2.51 |
| 2 | 94 | 14.96 | 13.39–16.26 | 0.62 | 4.17 |
| Length of nasals (LN) ($F = 20.08$) | | | | | |
| 15 | 14 | 7.25 | 6.60–8.30 | 0.47 | 6.40 |
| 16 | 20 | 7.29 | 6.40–8.10 | 0.45 | 6.20 |
| 9 | 21 | 7.41 | 6.50–8.10 | 0.39 | 5.26 |
| 8 | 25 | 7.50 | 6.60–8.60 | 0.42 | 5.64 |
| 10 | 24 | 7.51 | 6.90–7.80 | 0.29 | 3.81 |
| 3 | 50 | 7.53 | 6.80–8.40 | 0.38 | 5.07 |
| 17 | 23 | 7.56 | 6.60–8.50 | 0.51 | 6.69 |
| 6 | 12 | 7.58 | 6.60–8.40 | 0.53 | 7.03 |
| 5 | 17 | 7.60 | 6.40–8.60 | 0.56 | 7.37 |
| 11 | 29 | 7.64 | 6.30–8.60 | 0.52 | 6.78 |
| 7 | 19 | 7.74 | 6.60–8.90 | 0.55 | 7.08 |
| 13 | 24 | 7.75 | 7.00–8.60 | 0.43 | 5.56 |
| 12 | 28 | 7.75 | 7.00–8.60 | 0.41 | 5.27 |
| 4 | 11 | 7.76 | 7.00–8.30 | 0.38 | 4.86 |
| 14 | 18 | 7.97 | 7.20–8.80 | 0.42 | 5.32 |
| 2 | 94 | 8.25 | 6.90–9.50 | 0.51 | 6.13 |
| 1 | 28 | 8.59 | 6.90–9.40 | 0.57 | 6.61 |

Table 2. Continued.

| Sample no. | n | Mean | Range | SD | CV |
|---|---|---|---|---|---|
| Length of incisive foramen (LIF) ($F = 14.52$) | | | | | |
| 15 | 14 | 4.24 | 3.80–4.60 | 0.23 | 5.53 |
| 4 | 11 | 4.25 | 3.90–4.50 | 0.19 | 4.51 |
| 9 | 21 | 4.25 | 4.00–4.60 | 0.15 | 3.61 |
| 3 | 50 | 4.31 | 4.00–4.70 | 0.16 | 3.80 |
| 8 | 25 | 4.32 | 3.90–4.70 | 0.20 | 4.68 |
| 10 | 24 | 4.32 | 4.10–4.70 | 0.18 | 4.05 |
| 17 | 23 | 4.33 | 4.00–4.60 | 0.19 | 4.27 |
| 5 | 17 | 4.34 | 3.80–4.70 | 0.24 | 5.53 |
| 16 | 20 | 4.35 | 4.00–4.60 | 0.17 | 3.99 |
| 11 | 29 | 4.35 | 3.80–4.80 | 0.20 | 4.58 |
| 6 | 12 | 4.36 | 3.80–4.80 | 0.28 | 6.45 |
| 7 | 19 | 4.37 | 4.00–4.70 | 0.20 | 4.52 |
| 12 | 28 | 4.37 | 4.10–4.60 | 0.16 | 3.62 |
| 13 | 24 | 4.38 | 4.10–4.70 | 0.16 | 3.54 |
| 14 | 18 | 4.48 | 4.00–4.80 | 0.19 | 4.23 |
| 2 | 94 | 4.63 | 4.00–5.00 | 0.22 | 4.69 |
| 1 | 28 | 4.66 | 4.30–5.00 | 0.21 | 4.47 |
| Zygomatic breadth (ZB) ($F = 29.31$) | | | | | |
| 6 | 12 | 10.12 | 9.33–10.76 | 0.35 | 3.42 |
| 4 | 11 | 10.13 | 9.79–10.67 | 0.28 | 2.75 |
| 17 | 23 | 10.14 | 9.59–10.55 | 0.28 | 2.78 |
| 8 | 25 | 10.17 | 9.54–10.66 | 0.32 | 3.16 |
| 10 | 24 | 10.18 | 9.65–10.65 | 0.24 | 2.39 |
| 16 | 20 | 10.19 | 9.63–10.93 | 0.34 | 3.37 |
| 9 | 21 | 10.19 | 9.79–10.64 | 0.23 | 2.28 |
| 12 | 28 | 10.23 | 9.71–10.86 | 0.28 | 2.76 |
| 3 | 50 | 10.26 | 9.78–10.98 | 0.30 | 2.88 |
| 11 | 29 | 10.27 | 9.17–10.99 | 0.39 | 3.77 |
| 7 | 19 | 10.30 | 9.84–10.85 | 0.29 | 2.83 |
| 15 | 14 | 10.31 | 9.89–10.99 | 0.27 | 2.65 |
| 14 | 18 | 10.34 | 9.66–11.18 | 0.33 | 3.21 |
| 13 | 24 | 10.38 | 10.01–11.10 | 0.29 | 2.80 |
| 5 | 17 | 10.50 | 9.76–11.27 | 0.43 | 4.09 |
| 1 | 28 | 10.90 | 10.19–11.40 | 0.29 | 2.69 |
| 2 | 94 | 10.97 | 9.99–11.96 | 0.34 | 3.07 |
| Length of molar tooth row (AL) ($F = 18.58$) | | | | | |
| 10 | 24 | 3.11 | 2.80–3.40 | 0.14 | 4.48 |
| 15 | 14 | 3.11 | 3.00–3.40 | 0.14 | 4.34 |
| 9 | 21 | 3.12 | 3.00–3.30 | 0.09 | 2.85 |
| 11 | 29 | 3.13 | 2.80–3.40 | 0.14 | 4.36 |
| 3 | 50 | 3.14 | 2.90–3.40 | 0.12 | 3.92 |
| 4 | 11 | 3.15 | 3.00–3.40 | 0.13 | 4.11 |
| 8 | 25 | 3.16 | 3.00–3.30 | 0.10 | 3.27 |
| 12 | 28 | 3.17 | 2.90–3.40 | 0.13 | 4.10 |
| 17 | 23 | 3.17 | 3.00–3.50 | 0.11 | 3.58 |
| 6 | 12 | 3.18 | 3.10–3.30 | 0.08 | 2.37 |
| 13 | 24 | 3.19 | 3.00–3.50 | 0.14 | 4.33 |
| 7 | 19 | 3.19 | 3.00–3.40 | 0.10 | 3.04 |
| 5 | 17 | 3.22 | 3.00–3.40 | 0.11 | 3.34 |
| 14 | 18 | 3.23 | 3.00–3.40 | 0.13 | 4.11 |
| 16 | 20 | 3.28 | 3.00–3.50 | 0.12 | 3.69 |
| 2 | 94 | 3.36 | 3.10–3.80 | 0.11 | 3.36 |
| 1 | 28 | 3.40 | 3.00–3.60 | 0.14 | 4.12 |

Table 2. Continued.

| Sample no. | n | Mean | Range | SD | CV |
|---|---|---|---|---|---|
| Breadth of rostrum (BR) ($F = 9.08$) | | | | | |
| 15 | 14 | 3.00 | 2.77–3.48 | 0.19 | 6.44 |
| 8 | 25 | 3.18 | 2.89–3.51 | 0.18 | 5.51 |
| 12 | 28 | 3.19 | 2.92–3.39 | 0.12 | 3.85 |
| 3 | 50 | 3.20 | 2.85–4.16 | 0.23 | 7.21 |
| 17 | 23 | 3.25 | 2.92–3.51 | 0.14 | 4.42 |
| 9 | 21 | 3.25 | 2.89–3.51 | 0.17 | 5.14 |
| 4 | 11 | 3.27 | 3.06–3.53 | 0.14 | 4.36 |
| 14 | 18 | 3.28 | 3.04–3.65 | 0.19 | 5.77 |
| 7 | 19 | 3.28 | 3.02–3.44 | 0.11 | 3.36 |
| 11 | 29 | 3.29 | 3.07–3.70 | 0.14 | 4.23 |
| 16 | 20 | 3.29 | 3.07–3.49 | 0.12 | 3.64 |
| 13 | 24 | 3.30 | 2.89–3.62 | 0.17 | 5.10 |
| 10 | 24 | 3.31 | 2.99–3.51 | 0.14 | 4.12 |
| 6 | 12 | 3.32 | 3.11–3.61 | 0.14 | 4.29 |
| 5 | 17 | 3.39 | 3.05–3.82 | 0.20 | 6.01 |
| 1 | 28 | 3.41 | 2.40–3.88 | 0.25 | 7.21 |
| 2 | 94 | 3.43 | 3.13–3.90 | 0.18 | 5.32 |
| Length of palate (LP) ($F = 17.91$) | | | | | |
| 10 | 24 | 7.82 | 7.10–8.50 | 0.36 | 4.63 |
| 9 | 21 | 7.84 | 7.50–8.20 | 0.22 | 2.81 |
| 4 | 11 | 7.88 | 7.70–8.00 | 0.12 | 1.48 |
| 12 | 28 | 7.89 | 6.50–8.60 | 0.39 | 4.96 |
| 15 | 14 | 7.89 | 7.50–8.30 | 0.27 | 3.39 |
| 6 | 12 | 7.92 | 7.40–8.50 | 0.31 | 3.92 |
| 3 | 50 | 7.93 | 7.50–8.50 | 0.25 | 3.21 |
| 8 | 25 | 7.93 | 7.10–8.60 | 0.30 | 3.80 |
| 11 | 29 | 7.93 | 7.30–8.60 | 0.33 | 4.10 |
| 17 | 23 | 7.96 | 7.50–8.70 | 0.28 | 3.51 |
| 16 | 20 | 8.00 | 7.30–8.50 | 0.33 | 4.10 |
| 13 | 24 | 8.05 | 7.70–8.50 | 0.23 | 2.84 |
| 5 | 17 | 8.05 | 7.30–8.90 | 0.40 | 4.95 |
| 7 | 19 | 8.14 | 7.00–8.50 | 0.34 | 4.20 |
| 14 | 18 | 8.18 | 7.70–8.80 | 0.32 | 3.87 |
| 2 | 94 | 8.44 | 7.50–9.10 | 0.32 | 3.76 |
| 1 | 28 | 8.58 | 7.70–9.20 | 0.34 | 3.91 |

Francisco Bay area. The majority of mice in this study fall into age classes 2, 3, and 4. We decided to include animals of age class 6 in the samples used in the final taxonomic analyses because they do not consistently differ significantly from younger animals, and only a few individuals of this age class occur in any one sample.

## Geographic Variation

Analysis of variance (ANOVA) detected statistically significant ($P < 0.0003$) differences among the 17 samples for all 11 characters (Table 2), thus invalidating the null hypothesis of no statistically significant geographic variation among populations. Because all characters show significant interpopulation heterogeneity, it is appropriate to use them in further multivariate procedures. The greatest interlocality variation ($F$-ratios > 14) occurs in ZB, LN, LBC, AL, LP, GL, and LR; whereas IW, DBC, and BR exhibit the least variation ($F$-ratios < 10; Table 2). Western harvest mice from Santa Catalina and Santa Cruz islands average larger than specimens from other localities in 9 of 11 variables (81.8%); mice from Goleta and Devereux sloughs, Playa Del Rey, and San Clemente Island average smaller than other populations for 5–7 of 11 characters (45.5–63.6%) (Table 2). Multivariate analysis of variance (MANOVA) revealed that statistically significant differences ($F$ transformation of Wilk's lambda statistic = 5.87; d.f. = 176, 3946; $P < 0.0001$) exist among the 17 samples. Therefore, it is appropriate to investigate the dispersion of these samples within discriminant space.

The mean centroids for each of the 17 samples are plotted on the first three canonical variate axes (Fig. 5). Circles representing 95% confidence limits (Pimentel and Smith, 1986b) are drawn around each

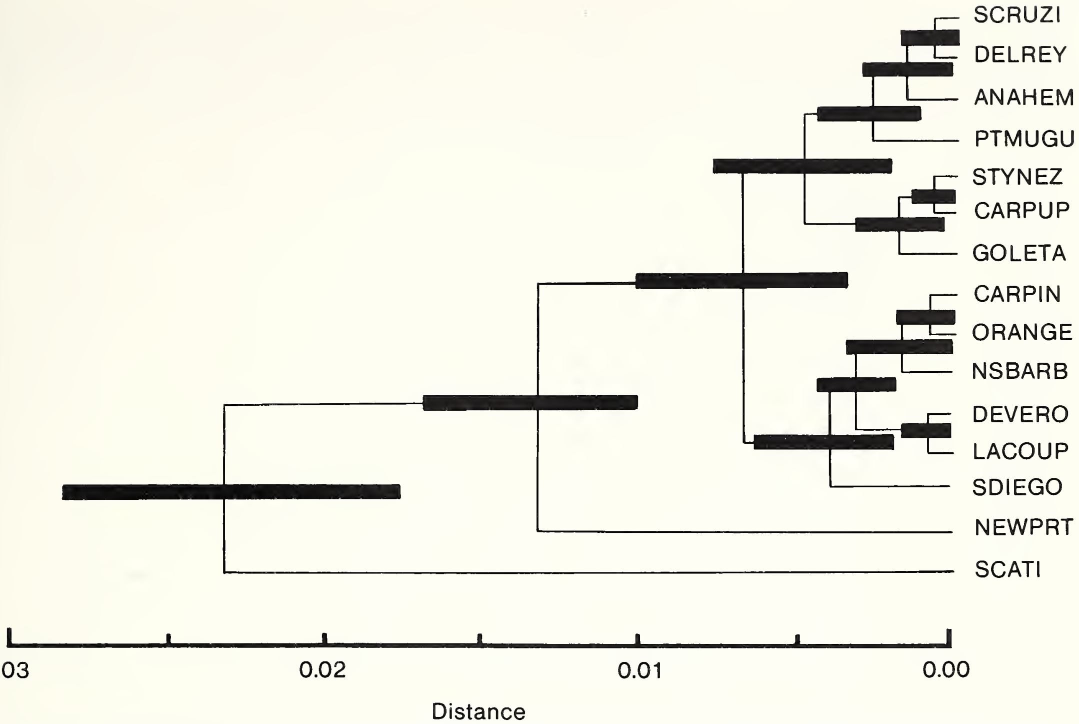

**Figure 3.** UPGMA phenogram constructed from Nei's distance values. Bars denote standard errors of the branch lengths.

centroid. The variance–covariance matrix yielded 11 canonical variates from among the 11 cranial characters used for all 17 samples. Only the first six canonical variates exhibit statistically significant ($\chi^2$, $P < 0.017$) morphological variation. The first three axes account for a combined total of 84.6% of the total phenetic variation (Table 4). Although canonical variates 4–6 are also significant ($P \leq 0.02$), each provides little additional discrimination between the localities; axes 7–11 account for less than 5% of the total between-group variation. Therefore, there is little distortion of the phenetic distances between

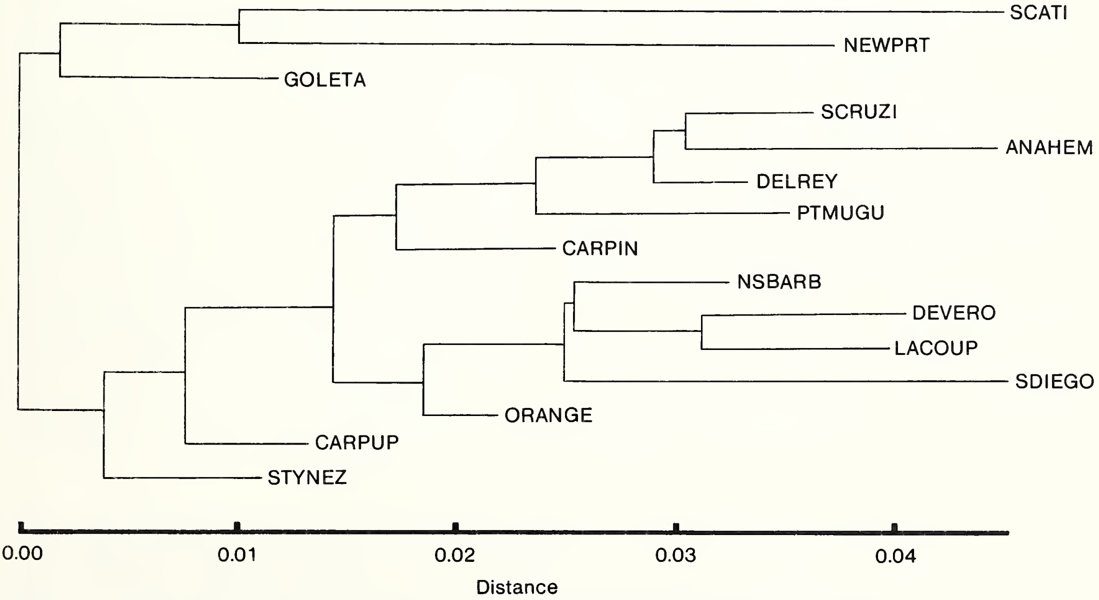

**Figure 4.** Distance-Wagner tree based on Rogers' distance values and rooted at the midpoint.

Table 3. Cranial variables in *Reithrodontomys megalotis* from southern California that exhibit significant ontogenetic variation. Statistically homogeneous subsets are derived from the Student-Newman-Keuls multiple range test and are shown by lines below the means for each age category. Any age categories underlined together are not significantly different ($P > 0.05$) from one another. Character acronyms are described in the Methods section. Age classes 0 and 1 were dropped prior to analysis because of insufficient sample size. Age classes 5 and 6 are combined.

| | Age class | | | | | |
|---|---|---|---|---|---|---|
| Character | 2 | 3 | 4 | 5 | *F*-ratio | Probability |
| Santa Catalina Island (sample 2, n = 93) | | | | | | |
| GL | 20.82 | 21.06 | 21.65 | 22.06 | 12.48 | 0.000 |
| LR | 6.76 | 6.77 | 7.02 | 7.30 | 7.51 | 0.000 |
| LN | 8.30 | 8.18 | 8.55 | 8.82 | 5.83 | 0.001 |
| ZB | 10.87 | 10.92 | 11.09 | 11.22 | 3.82 | 0.013 |
| BR | 3.30 | 3.47 | 3.50 | 3.48 | 7.66 | 0.000 |
| n | 27 | 38 | 19 | 9 | | |
| Santa Barbara County (samples 8 and 11, n = 51) | | | | | | |
| GL | 19.76 | 20.09 | 20.20 | 20.82 | 4.95 | 0.005 |
| DBC | 6.54 | 6.42 | 6.44 | 6.67 | 4.42 | 0.008 |
| LR | 6.19 | 6.37 | 6.48 | 6.63 | 3.04 | 0.038 |
| ZB | 10.02 | 10.20 | 10.35 | 10.52 | 3.99 | 0.013 |
| LP | 7.77 | 7.92 | 8.06 | 8.16 | 3.11 | 0.035 |
| n | 10 | 27 | 5 | 9 | | |

populations if the character space is reduced from 11 dimensions to only three.

The contributions of individual characters to the separation of centroids are depicted in Figure 5 by the magnitude and direction of the character vectors. With the exception of GL and IW, the remaining variables load positively on the first axis (Table 4, Fig. 5), suggesting that this represents a size axis. There were only a few variables that contributed a significant proportion of their variance to subsequent axes (Table 4, Fig. 5). Characters with more than 50% of their variance explained on the first axis were ZB, AL, DBC, and LN (Table 4). The only character on the second axis to have more than 50% of its variance explained is LBC (98%), whereas GL, LIF, and LP each contribute more than 35% of their variance to the second axis. On the third axis only LR had more than 50% of its variance explained, whereas IW had about 30% of its variance explained. On the remaining axes there were no characters with more than 40% of their variance explained.

Considerable phenetic overlap of the populations is evident in the plots of the first three canonical variates (Fig. 5). The overlapping confidence circles suggest that there is little significant variation among the southern California harvest mouse populations and that only small-scale differentiation is occurring. Canonical variate 1, which reflects overall size, accounts for 53.7% of the variation. Two of the island localities (Santa Cruz and Santa Catalina islands) have animals divergent in size (CV-1 in Fig. 5), but not in shape (CV-2 and CV-3 in Fig. 5), from those in adjacent mainland localities; this is consistent with the results of the SNK multiple-range tests (Table 2). When the first axis is eliminated by plotting the second against the third (Fig. 5B), the two island samples are indistinguishable from the remaining mainland samples. Thus, despite the magnitude of size differences exhibited by these two island samples, both populations still maintain the same basic skull shape as do mainland populations. There are no other distinct groupings of population samples in Figure 5 that are consistent with geography or with currently accepted taxonomy. Samples from the salt marshes of southern California (samples 3–6) currently allocated to *R. m. limicola* are indistinguishable on both the size (CV-1 in Fig. 5) and shape (CV-2 and 3 in Fig. 5) axes from other southern California harvest mouse populations (samples 7–17).

The degree of phenetic overlap of the 17 samples

⟶

**Figure 5.** Discriminant function plots of the first three canonical vectors. Circles represent 95% confidence limits about the mean centroid. Numbers refer to samples described in Figure 1 and in the Appendix. Contributions of individual characters to the separation of locality centroids are indicated by the magnitude and direction of the character vectors. For clarity, only the largest vectors are depicted.

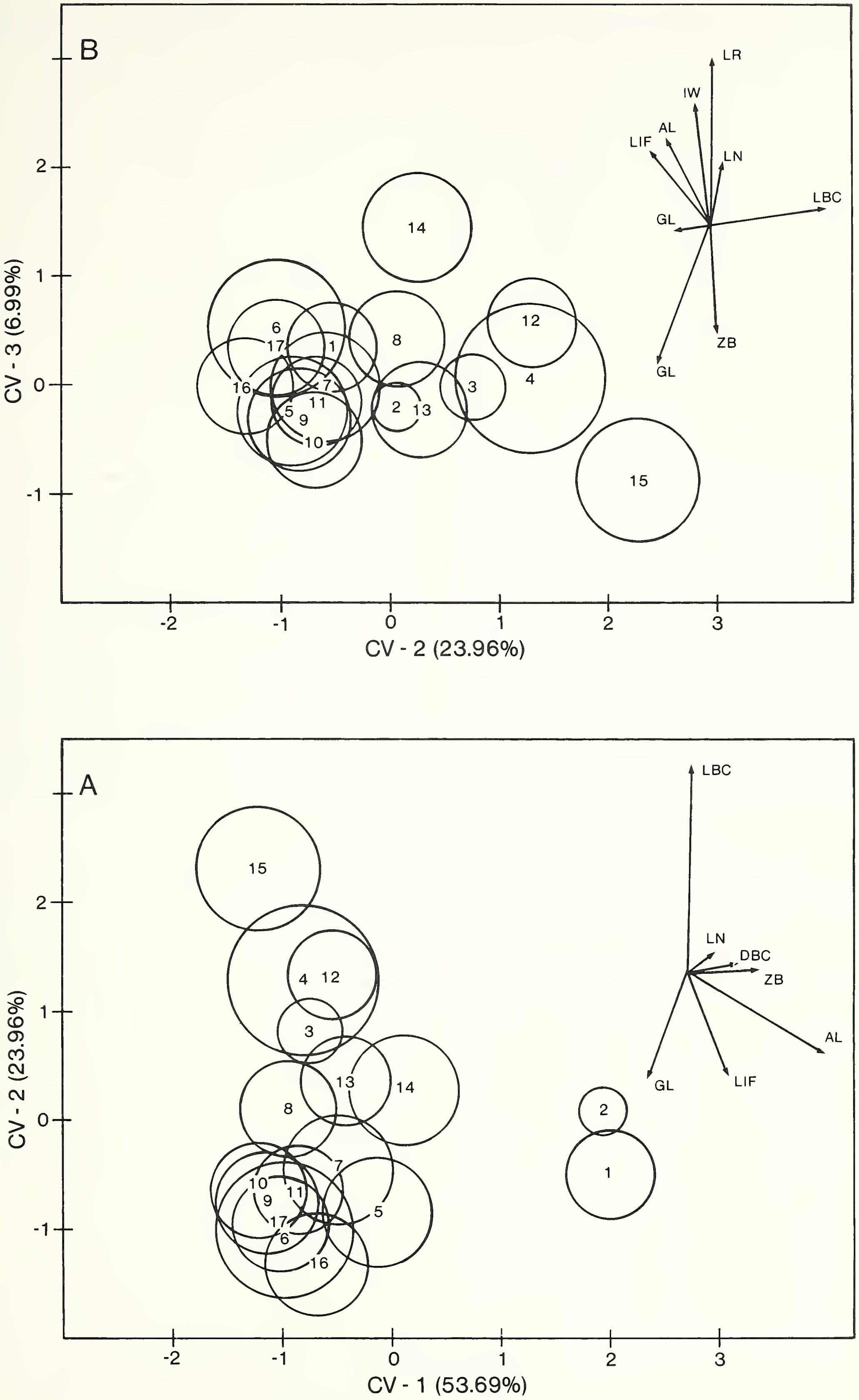
B
LR
IW
AL
LIF
LN
LBC
GL
ZB
GL
14
6
17
1
8
12
4
16
7
11
5
9
10
2
13
3
15
2
1
0
-1
CV - 3 (6.99%)
-2
-1
0
1
2
3
CV - 2 (23.96%)
A
LBC
LN
DBC
ZB
AL
GL
LIF
15
4
12
3
13
14
8
2
1
7
10
11
9
5
17
6
16
2
1
0
-1
CV - 2 (23.96%)
-2
-1
0
1
2
3
CV - 1 (53.69%)

Table 4. Character loadings and percent of overall morphological variance explained for the first six canonical vectors of interlocality phenetic variation in *Reithrodontomys megalotis* from southern California.

| | Canonical variates | | | | | |
|---|---|---|---|---|---|---|
| Character | 1 | 2 | 3 | 4 | 5 | 6 |
| GL | −0.215 | −0.348 | −0.467 | 0.005 | 0.179 | −0.233 |
| DBC | 0.294 | 0.036 | −0.082 | −0.111 | −0.205 | 0.450 |
| IW | −0.062 | −0.079 | 0.386 | 0.219 | −0.633 | −0.140 |
| LR | 0.066 | 0.038 | 0.544 | 0.143 | 0.210 | 0.500 |
| LBC | 0.050 | 0.760 | 0.050 | −0.014 | −0.110 | −0.055 |
| LN | 0.158 | 0.086 | 0.192 | −0.335 | 0.020 | −0.177 |
| LIF | 0.215 | −0.355 | 0.240 | −0.108 | −0.300 | 0.323 |
| ZB | 0.416 | 0.026 | −0.356 | 0.068 | 0.081 | 0.303 |
| AL | 0.762 | −0.271 | 0.277 | 0.674 | −0.198 | −0.420 |
| BR | 0.138 | −0.188 | −0.025 | −0.511 | −0.573 | −0.121 |
| LP | 0.111 | −0.221 | 0.170 | 0.275 | 0.061 | −0.227 |
| Percent | 53.69 | 23.96 | 6.99 | 4.98 | 3.06 | 2.39 |

was further assessed by comparing the proportion of individuals from each locality that was misclassified by the discriminant function analysis. Of 457 specimens, a total of 171 (37%) were classified correctly to their *a priori* designated samples by the classification procedure of the discriminant function analysis (Table 5). The degree of morphological overlap among mainland and island locality samples in southern California is evident in the percentage of misclassified individuals, which averaged 63%. The most distinctive locality samples were from SCLEMI (14% misclassified), SCRUZI and LACOUP (39% misclassified each), and DELREY and SCATI (45% misclassified each), whereas the least distinctive locality samples were NSBARB and SSBARB (localities 8 and 11), which had 96% and 90% of their specimens misclassified, respectively.

Of the 11 Santa Cruz Island specimens that were misclassified, five were classified with Santa Catalina Island (sample 2), three with the Los Angeles County upland site (sample 14), and one each with San Clemente Island (sample 15) and Orange County upland (sample 16). Of the 42 Santa Catalina Island specimens that were misclassified, 20 (48%) were classified with Santa Cruz Island whereas 16 (38%) were classified with Los Angeles and Orange County mainland localities (samples 4, 5, 14, and 16). Only two of the 14 San Clemente Island specimens were misclassified, one with the Goleta Slough sample (sample 10) and one with the Carpinteria upland

Table 5. Geisser classification of individual western harvest mice from southern California (n = 457). Rows are actual groups and columns are predicted groups. See Appendix for explanation of sample acronyms.

| | | | | Predicted locality | | | | |
|---|---|---|---|---|---|---|---|---|
| Actual locality | | n | Percent classified correctly | 1 | 2 | 3 | 4 | 5 |
| SCRUZI | 1 | 28 | 61 | 17 | 5 | | | |
| SCATI | 2 | 94 | 55 | 20 | 52 | | 1 | 9 |
| PTMUGU | 3 | 50 | 6 | | | 3 | 7 | 6 |
| DELREY | 4 | 11 | 55 | | | | 6 | |
| ANAHEM | 5 | 17 | 41 | 2 | | | | 7 |
| NEWPRT | 6 | 12 | 25 | | 1 | 1 | | |
| STYNEZ | 7 | 19 | 42 | 1 | 1 | | 1 | |
| NSBARB | 8 | 25 | 4 | | | 3 | | 1 |
| DEVERO | 9 | 21 | 38 | | | | | 1 |
| GOLETA | 10 | 24 | 33 | | | | | |
| SSBARB | 11 | 29 | 10 | 2 | | | 2 | 2 |
| CARPUP | 12 | 28 | 50 | | 1 | 1 | 5 | |
| CARPIN | 13 | 24 | 21 | | 1 | 1 | | 2 |
| LACOUP | 14 | 18 | 61 | 1 | 1 | | 2 | |
| SCLEMI | 15 | 14 | 86 | | | | | |
| ORANGE | 16 | 20 | 50 | | 1 | | | 2 |
| SDIEGO | 17 | 23 | 13 | | | | | |

sample (sample 12). Of the 136 island specimens, 29 (21%) were misclassified with mainland localities, whereas 25 (7.8%) of the 321 mainland specimens were misclassified with island localities. Specimens of *R. m. limicola* (samples 3–6) do not show a consistent pattern of misclassification. Of the 72 specimens misclassified in these four localities, only 17 (24%) were misclassified with other *R. m. limicola* populations (Table 5). Thus, the low proportions of correctly classified individuals in this discriminant function analysis suggest that the degree of phenetic overlap among the samples is great and that there are only gradual phenetic changes occurring among the 17 southern California samples.

## DISCUSSION

### GENETIC VARIABILITY

Population variation ($F_{ST}$) of 8.1% among the 15 populations of *R. megalotis* is indicative of low to moderate variation in mammals (Wright, 1978; Hartl, 1988). This value is comparable to that found among western populations of *Peromyscus maniculatus* (Calhoun *et al.*, 1988) but lower than that value calculated for populations across the range of *P. maniculatus* (Avise *et al.*, 1979). Our $F_{ST}$ is similar to the value calculated for populations of *Cynomys mexicanus* (McCullough and Chesser, 1987) and for populations of *C. ludovicianus* within geographically separated regions (Chesser, 1983). The inbreeding coefficients ($F_{IS} = 0.245$, $F_{IT} = 0.307$) are rather high; this might be explained by the fact that of the 93 cases where a population is heterozygous for a particular locus, 14 of these do not conform to Hardy-Weinberg equilibrium (Table 1). In most of these 14 cases there is the occurrence of a "rare" allele in the homozygous state or in heterozygosity with another rare allele.

From the $F_{ST}$ value, one can calculate the number of dispersers among populations, assuming genetic drift and dispersal are in equilibrium (Wright, 1969). The result is 2.84 individual dispersers per generation among the 15 populations of *R. megalotis* examined. This is comparable to values found in other rodents (McCullough and Chesser, 1987; Calhoun *et al.*, 1988). With the exception of the island populations, *R. megalotis* probably was distributed continuously throughout southern California prior to the urbanization of the last 100 years. This distribution would account for the high estimated rate of dispersal among populations, in spite of the great distance between sample sites.

Average heterozygosity has not been characterized from allozyme data for any species of *Reithrodontomys* until now (Arnold *et al.*, 1983; Nelson *et al.*, 1984), but the heterozygosity levels we detected in southern California populations of *R. megalotis* fall within levels calculated for *Peromyscus* species in California (Avise *et al.*, 1974, 1979; Smith, 1979; Gill, 1980; Calhoun *et al.*, 1988) and elsewhere in North America (Selander *et al.*, 1971; Smith *et al.*, 1973; Kilpatrick and Zimmerman, 1975), with the exception of the population from Santa Cruz Island. Insular populations of mammals have, on the average, 42% less genetic variability (measured by heterozygosity) than mainland populations of the same species (Kilpatrick, 1981). The average heterozygosity across all mainland samples examined herein is 0.043, whereas

**Table 5. Continued.**

| Predicted locality | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| | 1 | | | | | | | 3 | 1 | 1 | |
| | 2 | | | 1 | 1 | | 1 | 4 | | 2 | 1 |
| | 2 | 1 | 3 | 3 | 1 | 11 | 1 | 1 | 8 | 2 | 1 |
| | | | | | | 2 | | | 1 | 2 | |
| 3 | 1 | 1 | | | | | | | | 3 | |
| 3 | | | 1 | | 1 | | | 1 | | 2 | 2 |
| 2 | 8 | | 2 | 1 | 1 | | | | | 2 | |
| 1 | 1 | 1 | 2 | 2 | | 4 | 2 | 1 | 1 | 2 | 4 |
| | 1 | | 8 | 5 | 3 | | | | | 2 | 1 |
| | 3 | | 5 | 8 | 2 | | 3 | | | 1 | 2 |
| 2 | 2 | 2 | 4 | 6 | 3 | | | 1 | | 2 | 1 |
| | | 1 | | 2 | | 14 | | 2 | 1 | | 1 |
| | 3 | | | 4 | 1 | 6 | | | 1 | | |
| 1 | | | | 1 | | | | 11 | 1 | | |
| | | | | 1 | | 1 | | | 12 | | |
| | 1 | 1 | 3 | | | | 1 | | | 10 | 1 |
| 7 | 2 | | 4 | | 3 | | | | | 4 | 3 |

heterozygosity of the Santa Cruz Island sample is only 0.003. This primarily is the result of an increase in the number of monomorphic loci and the absence of most rare and low-frequency alleles found on the mainland and may be interpreted as the result of founder effect (Kilpatrick, 1981; Berry, 1986). This phenomenon is not evident in the sample from Santa Catalina Island ($H = 0.044$; $P = 20\%$). The effect of genetic drift appears to have a strong influence on this population, however, as seen in the predominance of alternate alleles for two loci (Pep-$D^B$ and $ADA^A$).

Neither the cluster analysis nor the distance-Wagner analysis provides results concordant with geographic or ecological patterns. There are no evident north–south clinal trends, nor are there any wetland–upland patterns of clustering. The distance and similarity data do not support the recognition of a subspecies limited to coastal salt marshes, nor do they support the recognition of a unique subspecies on Santa Cruz Island (Nei's $I$ of 0.999 with the sample from DELREY). The Santa Catalina Island sample has the lowest identity value (0.977) with other samples of harvest mice (Fig. 3), but again, this is very high for a population that has been classified as a distinct subspecies.

Standard errors of the branch lengths of the UPGMA dendrogram overlap below the 0.01 level, suggesting that the branch points below the 0.01 level are not reliable (Fig. 3; Nei *et al.*, 1985). The standard error of the branch points for the samples from Newport Bay and Santa Catalina Island nearly overlap and must be considered with caution. The possibility exists that a UPGMA tree calculated from electrophoretic data can deviate greatly from the true evolutionary tree. As the number of loci examined increases, the likelihood that the UPGMA tree deviates from the true tree decreases (Nei *et al.*, 1983). Having considered 30 loci, we are confident that our tree is a reasonable representation of the relationships among the populations. Therefore, we conclude that the distance values among the populations we examined are so low that they reflect extremely close relationship and little genetic divergence in western harvest mice in southern California.

## MORPHOLOGIC VARIATION

Canonical variate analysis of the morphologic data reveals that, aside from the two island populations, there is little geographic variation in overall cranial morphology among southern California populations of *R. megalotis*. There is a high degree of phenetic overlap among the 17 samples with no clear associations evident among size, geography, ecology, or currently accepted taxonomy. This is best exemplified by the low proportions (37%) of correctly classified individuals in the discriminant function analysis and in the extent to which the 17 localities overlap in multivariate space (Fig. 5). These data suggest that only gradual small-scale phenetic changes have taken place within *R. megalotis* populations in this region. This pattern of morphologic variation is probably attributable, at least in part, to the absence of any major geographic barriers in the region that would result in morphologic divergence.

Analysis of cranial characters indicates some separation (size only) of the Santa Cruz and Santa Catalina island populations from other samples. As there are no distinct shape differences, these populations may have been isolated from parental populations of *R. megalotis* fairly recently. Misclassifications of Santa Cruz and Santa Catlina island individuals (Table 5) tend to be to the other island, rather than to mainland or San Clemente Island samples. These data, when viewed in concert with the degree of phenetic overlap observed between the Santa Cruz and Santa Catalina island populations (Fig. 5), suggest that either gene flow has occurred between these two islands, or parallel (or convergent) evolution has occurred.

Island populations tend to be subject to strong directional selection because of their isolation and reduced gene flow with the mainland. Grant (1979b) suggested that the reduction in phenotypic variation in isolated populations is due both to a reduction in gene flow and to differentiation that results from random genetic drift and directional selection. By identifying characters or suites of characters that exhibit reduced variability, Zink (1986) suggested that it may be possible to identify important fitness traits. Also, by examining intraspecific morphological variation, it may be possible to determine whether any discrete, morphologically uniform samples exist that correspond to evolutionary units that may warrant subspecific classification (Cracraft, 1983; Zink, 1986).

All of the coefficients of variation (CVs) for cranial characters used in this study (Table 2) are less than 10%. In general, intermeatus width (IW) and characters of the rostrum (LN, LR, and BR) tend to be more variable than the other cranial characters (Table 2), whereas levels of variability are lower and fairly uniform among localities for greatest length of skull (GL), depth of brain case (DBC), and zygomatic breadth (ZB). The higher CVs obtained for IW, LN, LR, and BR could be indicative of inherent variation present in the populations studied or could be a result of higher than average measurement error with these four characters.

Two of the island samples (Santa Cruz and Santa Catalina islands) exhibit slightly higher levels of variability (mean CVs, 4.85 and 4.76, respectively) than the other island (San Clemente Island; mean CV, 4.49) and most of the mainland populations (mean CVs, 3.43–4.56). This contrasts with results obtained by Aquadro and Kilpatrick (1981) for *Peromyscus* on islands off the coast of Maine. Based on mean CV, the San Clemente Island sample did not show a consistent departure in variability from the mainland samples. There are no other consistent patterns of variation in mean CVs for cranial characters that might correspond to ecological, environmental, or geographic parameters. Further, there are no clines evident in the CVs for cranial characters used in this study.

A number of studies have correlated morphological variability with niche breadth (Van Valen, 1965; Rothstein, 1973; Grant, 1979a; Power, 1983; Schnell *et al.*, 1986) or with changes in interspecific competition (Schoener, 1970). Deer mice occur sympatrically with harvest mice in very low densities on the mainland but are abundant on the California Channel Islands. It is possible that the increased density of deer mice caused harvest mice on Santa Cruz and Santa Catalina islands to shift their niche and exploit a wider variety of foods. The slight increase in morphological variability and the increase in overall size observed in these island populations may be related to this increase in niche width.

Gigantism, accompanied by an increase in morphological variability, is a common phenomenon seen in small mammal species on islands, particularly in cricetid rodents (Foster, 1964; Lomolino, 1985). Lomolino (1985) explains this as the result of competitive release, which has an increasing effect as the size of the species decreases. Mainland populations of harvest mice in southern California are sympatric with many rodent species (depending on the locality), including sciurids, heteromyids, cricetids, and arvicolids, whereas island populations are sympatric with only two species, *Spermophilus beecheyi* (on Santa Catalina Island only) and *Peromyscus maniculatus*. This, too, may be a contributing factor to the increase in size observed in harvest mouse populations on Santa Cruz and Santa Catalina islands.

## COVARIATION OF MORPHOLOGICAL AND PROTEIN CHARACTER SETS

Mayr (1963) suggested that natural selection acts on the total genotype through the phenotype rather than on individual genes or phenetic characters. However, Schnell and Selander (1981) suggested that protein and morphologic characters evolve independently because they are subject to different types of evolutionary pressures. The exact relationships between phenotypic and genotypic changes still are not well understood. Specifically, we know little about the heritability of observed patterns of morphometric size and shape variation (Atchley *et al.*, 1981), and we do not know the role that genetic variability plays in the structuring of phenotypic variability. Without data on the heritability and number of loci that contribute genetic variance to a particular morphological trait, it is impossible to determine whether allozymes and morphologies evolve independently (Zink, 1986). What is known is that most morphological traits are polygenic (controlled by many structural and regulatory genes) (Lewontin, 1974) and that the majority of genes are pleiotropic (affecting many different characters of the phenotype) (Wright, 1980). Thus, the genotype and the phenotype are intimately intertwined systems that are composed of interacting components (Cheverud, 1982).

Racial affinities within a taxon can be examined in a number of ways, using biochemical, cytological, and phenetic data. However, analyses based on one data set, either phenetic or genetic, can give patterns of divergence or rates of change between populations that are different from those obtained from a comparative analysis of more than one type of variation. For example, Berry and Peters (1976), Pizzimenti (1976), Shvarts (1977), Schnell *et al.* (1978), Gill (1980), and Aquadro and Kilpatrick (1981) all failed to find concordance between electrophoretic variability and detectable levels of morphological or karyotypic variation. Selection may be operating in diverse ways at different levels (Schnell and Selander, 1981). There are, however, an increasing number of geographic variation studies on mammals that have found concordant patterns of relationships, based on biochemical, cytological, and morphological analyses (*e.g., Rattus*—Patton *et al.*, 1975; *Dipodomys*—Best, 1983; Best *et al.*, 1986; *Eutamias*—Sullivan, 1985; *Thomomys*—Smith and Patton, 1988). These studies have shown that operationally independent estimates of divergence may accurately reflect similar trends in genomic variability and phylogenetic relationships within a taxon.

In our study of western harvest mice from southern California, the results of the electrophoretic analyses generally were similar to the observed patterns of geographic variation delineated by the morphometric analyses. Both the genetic and the morphometric analyses demonstrate little geographic variation. Most populations cluster in no discernable geographic or taxonomic pattern. Samples from Santa Cruz and Santa Catalina islands were divergent in size from the other samples. The most divergent sample (Santa Catalina Island) also exhibited the greatest amount of genetic differentiation. The nature of this divergence can be explained by a nonclinal pattern of genic variation that is caused by the presence of uniquely fixed alleles and frequency differences at two loci. The absence of any significant genetic variation in the *R. megalotis* populations of southern California is probably a result of the absence of any major geographic barriers between populations in the region.

## HYPOTHESES ON ISLAND COLONIZATION

Questions persist regarding how and when harvest mice colonized the islands. Von Bloeker (1967) suggested that harvest mice were accidentally introduced to San Clemente Island in bales of hay during this century. Such a recent colonization would not provide the population enough time to adapt to local conditions, and in fact, the sample we examined demonstrated no substantial morphological divergence from the mainland populations. Conversely, the San Clemente Island sample had the highest percentage of correct Geisser classification (86%) of any sample included in this study (Pimentel and Smith, 1986b). This might be argued as evidence for some period of isolation and subsequent morphological differentiation, or it might be used as support for the founder effect. The fact that this species has only been collected from a small area on the island suggests that the latter case may be true; the population has not been on the island long enough to become well established and to have diverged from mainland populations but is still under the constraints of a founder effect and has low intrapopulation variability. Additional work on this population, including examination of allozymic variability, may shed some light on this question.

Harvest mouse populations on Santa Cruz and Santa Catalina islands show slight divergence from the mainland populations, the former only in cranial size and the latter in both cranial size and gene frequency at two loci. These data suggest a longer period of isolation (*i.e.*, perhaps since the last glacial episode, *ca.* 13,000 years BP) for these two islands than for the San Clemente Island population. Genetic interchange between the islands via Indian transport has been used to explain patterns of morphological variation in *Urocyon littoralis* (Collins, in press) and *P. maniculatus* (Gill, 1980). We do not feel that such a scenario is true for *R. megalotis* because of the low relative genic similarity of the samples, the extremely high similarity of the Santa Cruz Island sample to the coastal samples, and the lack of unique or rare alleles shared by the two island samples.

The question of when the islands were colonized by *R. megalotis* remains. Size divergence in two of the island samples suggests that western harvest mice were probably established on these islands prior to the last 100 years. Certainly Santa Catalina Island was colonized prior to the colonization of Santa Cruz Island. Besides the genetic evidence, there are ecological data to support this claim. Western harvest mice are far more abundant and widespread and are equally as common as *P. maniculatus* on Santa Catalina Island (Williams, 1986), whereas on Santa Cruz Island, harvest mice are limited to Prisoners' Harbor and the east end of the island and are caught in lower numbers (Bills, 1969; Williams, 1986).

Determining the time of colonization of the islands is extremely difficult. Geologic data do not support the existence of any land bridges between the mainland and any island, between northern and southern islands, or between any of the southern islands during the Pleistocene (Junger and Johnson, 1980; Vedder and Howell, 1980; Johnson, 1983). The Northern Channel Islands (Anacapa, Santa Cruz, Santa Rosa, and San Miguel) were connected as one superisland (Santarosae) several times during glacial episodes in the Pleistocene (Johnson, 1978). Santarosae reached its maximum size about 18,000 years BP when sea level was approximately 120 m below its present-day level. With the end of full glacial conditions, sea level began to rise. Anacapa Island separated from Santarosae first about 12,000 years BP, followed by Santa Cruz Island at 11,500 years BP, and finally by San Miguel Island at 9,500 years BP (Johnson, 1978).

Several lines of evidence refute a pre-Holocene colonization of Santa Cruz Island by *R. megalotis.* Although the mammalian fossil record from Anacapa, San Miguel, and Santa Rosa islands has been well documented, there are no known fossils of harvest mice from these islands (D.A. Guthrie, *in litt.*; Lipps, 1964; White, 1966; Walker, 1980). Santa Cruz Island has a poor fossil record, but because it was connected by a land bridge to Anacapa prior to 12,000 years BP and to Santa Rosa and San Miguel islands prior to 11,500 years BP, we would predict that *R. megalotis* would have been detected in those islands' fossil record if the species had then been present on Santarosae. Therefore, it is probable that harvest mice reached Santa Cruz Island since it last separated from the Santarosae Island mass. Although the high standard errors on the genic data preclude setting divergence times to the branch points of the islands (Nei, 1972; Nei *et al.*, 1985; Sarich, 1977), Santa Cruz Island allozymically is indistinguishable from the mainland. This also supports a recent, probably late Holocene, colonization.

Setting a time for the colonization of Santa Catalina Island by harvest mice is more problematic. This population shows some genetic distinctiveness, although the genetic distance from the mainland is still less than 2.3%. Genetic distance between mainland and Santa Catalina Island populations of *P. maniculatus* is far greater, averaging 6.2% (Gill, 1980). An analysis of restriction sites in mitochondrial DNA from four specimens of Santa Catalina Island populations of *R. megalotis* yielded only one polymorphism out of 78 sites examined, far lower than the number found in sympatric populations of *P. maniculatus* (Ashley and Wills, 1987; Ashley, 1989). Therefore, we believe that the population on Santa Catalina Island also is the result of a recent introduction, although this population has had a greater length of time to become adapted to the environment than has the population on Santa Cruz Island.

With access to the California Islands by land bridge ruled out, other means of transport must be considered. In southern California, rafting has been documented for *Lepus californicus;* one individual was found weak but alive on a kelp raft 63 km from the nearest point on the mainland and 24 km northwest of San Clemente Island (Prescott, 1959). Given the extent of the water barriers between the islands and the mainland, however, chances that the mice rafted to the island are less likely than colonization by human transport (Wenner and Johnson, 1980). The regular transport of supplies and material between the mainland and the islands by the Chumash and Gabrieleño Indians was extensive and began approximately 9000 years BP when the islands were first settled (King, 1971; Tartaglia, 1976; Hudson *et al.,* 1978). The Indians stored their plank canoes in marshes between voyages (Hudson *et al.,* 1978), providing ample opportunity for harvest mice to inadvertently stow away and be transported to the islands. This method of introduction appears to be the most plausible explanation for the presence of *R. megalotis* on the California Channel Islands.

## TAXONOMY

In studies of geographic variation, the naming of subspecies is not as important as deciphering the patterns of variation observed within a species. Like Barrowclough (1982:602), we believe that it is possible to identify infraspecific taxa if separate analyses of electrophoretic and morphometric variation "all delimit the same 'discrete structures' in multivariate space." However, in insular situations, where allopatric populations differ in only one character state, the use of a trinomial might not be warranted. We feel that when properly used to "identify those historical geographic units that represent opportunities for sustained evolutionary divergence" (Smith and Patton, 1988:174), the subspecies category is an important taxonomic category that is helpful to the study and understanding of evolutionary processes and models.

In the western harvest mouse, four subspecies (*R. m. catalinae, R. m. limicola, R. m. longicaudus,* and *R. m. santacruzae*) currently are recognized in southern California (Hall, 1981). With the exception of the two allopatric island populations, there are no discrete geographic barriers to gene flow that coincide with existing subspecies boundaries. Results of the genetic and phenetic analyses presented above indicate that within populations of *R. megalotis* in southern California there are no historical geographic units that warrant subspecific recognition. Rather, there exists broad phenetic overlap among the samples, suggesting that only gradual, small-scale phenetic change occurs among *R. megalotis* populations in mainland southern California.

In examining patterns of geographic variation, it is important to ask whether the observed geographic variation is the result of genetic change due to genetic drift, whether it is a plastic response to local environmental conditions, or whether it represents fundamental adaptive genetic change. Patton and Brylski (1987) have shown that body size in *Thomomys bottae* is an ecophenotypically plastic character, whereas shape differences are the products of long-term evolutionary divergence. In the case of *R. megalotis* on Santa Cruz and Santa Catalina islands, there has been a divergence from mainland populations in size but not in cranial shape. The lack of any underlying shape difference and the fact that there are no substantive genic criteria distinguishing the island samples from the mainland samples suggests that populations of *R. megalotis* in southern California are of one genetic stock. The size increase in the two island populations may be a phenotypic response to the unique environmental conditions present on the islands and not the product of long-term evolutionary divergence. The San Clemente Island population, which von Bloeker (1967) suggests was inadvertently introduced to the island during the 1930s in shipments of baled hay from San Diego County, has not shown a comparable shift in body size similar to that seen in the other two island populations. This suggests that harvest mice have been isolated on Santa Cruz and Santa Catalina islands for a longer period of time than they have been on San Clemente Island.

In the absence of any substantive genic or morphologic breaks across the geographic range of the western harvest mouse in southern California, we conclude that only one subspecies should be recognized. We recommend that the following nomenclatural adjustments be made. The name *R. m. longicaudus* (Baird, 1857), which has priority, would apply to all harvest mouse populations in southern California west of the foothills of the San Gabriel, San Bernardino, and San Jacinto mountain ranges, as well as on the Channel Islands. Following is a revised synonymy for this species in the southern California region.

### *Reithrodontomys megalotis longicaudus* (Baird)

*Reithrodon longicauda* Baird, 1857:451 (orig. desc.).
*Ochetodon longicauda:* Coues, 1874:186.
*Reithrodontomys pallidus* Rhoads, 1893:835 (orig. desc.).
*Reithrodontomys longicauda:* Allen, 1895:129.
*Reithrodontomys longicauda pallidus:* Allen, 1895: 131.
*Reithrodontomys klamathensis* Merriam, 1899:93 (orig. desc.).
[*Reithrodontomys*] *longicaudus:* Elliot, 1901:151.
*Rhithrodontomys catalinae* Elliot, 1904:246 (orig. desc.).
*Reithrodontomys megalotis longicauda:* Mearns, 1907:464.
*Reithrodontomys catalinae:* Howell, 1914:40.
*Reithrodontomys megalotis klamathensis:* Grinnell, 1913:303.
*Reithrodontomys megalotis longicaudus:* Howell, 1914:33.
*Reithrodontomys megalotis catalinae:* Grinnell, 1913:304.
*Reithrodontomys megalotis limicola* von Bloeker, 1932:133 (orig. desc.).
*Reithrodontomys megalotis santacruzae* Pearson, 1951:366 (orig. desc.).

**DIAGNOSIS.** *Reithrodontomys m. longicaudus* can be characterized as dark and small in size (total length, 124–163 mm), except for the populations on Santa Cruz and Santa Catalina islands, which are large bodied (total length, 152–178 mm). The color of the upperparts is mixed-blackish and ochraceous-buff with black predominating on the back of the neck and shoulders; the ventral surfaces are grayish white with a wash of ochraceous-buff, especially in the pectoral area. The sides are a brighter ochraceous-buff than the back, whereas the ears are the same color as the back with a wash of ochraceous hairs on their inner surfaces. The tail is bicolored, hair brown above and grayish white below. Color variation in *R. m. longicaudus* is considerable across the geographic range of the subspecies, with summer and winter pelages decidedly different. Lacking much of the black on the dorsal surface, fresh summer pelage is noticeably paler than that of fresh winter pelage.

**COMPARISONS.** *Reithrodontomys m. longicaudus* exhibits considerable geographic variation both in color and in size of skull. According to Howell (1914), this subspecies can be distinguished from *R. m. megalotis* by its small size and somewhat darker (more heavily washed with black), more intense colors. These two subspecies intergrade in a number of places along the edge of the deserts in southern California (Howell, 1914). Western harvest mice on Santa Cruz and Santa Catalina islands can be distinguished from other populations of *R. m. longicaudus* only by their slightly larger size. According to von Bloeker (1937), *R. m. distichlis* (from coastal marshes at Monterey Bay) can be distinguished from *R. m. longicaudus* by the former's smaller size and average darker dorsal coloration. The taxonomic validity of *R. m. distichlis* has been questioned by Pearson (1951), who could not distinguish specimens assigned to this taxon from upland *R. m. longicaudus* in the area. A more detailed assessment of the genetic and morphological characteristics of purported *R. m. distichlis* populations may find that, as for *R. m. limicola,* the characters originally used to identify this taxon are too slight and inconsistent to warrant its continued recognition.

**RANGE.** *Reithrodontomys megalotis longicaudus* is a broadly distributed subspecies of the western harvest mouse that ranges from southwestern Oregon southward throughout most of western California and along the coast into northwestern Baja California to about 32° N latitude (Howell, 1914; Hall, 1981). In California, *R. m. longicaudus* inhabits the greater part of western California east to the foothills of the Sierra Nevada, San Bernardino, and San Jacinto ranges, whereas *R. m. megalotis* can be found east of these mountain ranges, including most of the Great Basin, Mohave Desert, and Sonoran Desert regions of the state (Grinnell, 1933). Based on the results of this study, we are also including the introduced population of western harvest mice on San Clemente Island, as well as the harvest mice found in the coastal salt marshes of southern California and on Santa Cruz and Santa Catalina islands, within the range of *R. m. longicaudus.*

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## APPENDIX

### List of Specimens Examined

Localities for specimens of *Reithrodontomys megalotis longicaudus* examined in the morphometric and allozymic analyses are listed below by number, with acronyms in parentheses, and are indicated on the map (Fig. 1). Sample sizes for each analysis are indicated by numbers in parentheses as follows: m = morphometric sample, e = allozymic sample. A listing of the complete names for collections in which specimens are housed can be found in the acknowledgments; additional specimens were examined at the Natural History Museum of Los Angeles County (LACM) and the Santa Barbara Museum of Natural History (SBMNH). Frozen tissues are deposited in the Frozen Tissue Collection at the Natural History Museum of Los Angeles County. Voucher specimens for frozen tissues are deposited at LACM, SBMNH, UCSB, and the University of Kansas. All localities listed are in California.

**Locality 1 (SCRUZI; m = 28,** e = **20).** Santa Barbara Co., Santa Cruz Island: end Central Valley, NW airstrip (m = 2 LACM, 1 SBMNH; e = 3); E end Central Valley, E end airstrip (m = 3 SBMNH; e = 2); E end Central Valley, orchard E airstrip (m = 1 SBMNH; e = 1); E end Central Valley 0.1 mi. S dump (m = 2 LACM; e = 2); Prisoners' Harbor (m = 6 MVZ, 5 LACM, 7 SBMNH; e = 12); 1 mi. S Prisoners' Harbor (m = 1 LACM).

**Locality 2 (SCATI; m = 94, e = 15).** Los Angeles Co., Santa Catalina Island: no specific locality (m = 3 LACM, 12 MVZ); 2 mi. W Avalon (m = 1 SDMNH); Avalon (m = 1 MVZ, 3 SDMNH); 0.5 mi. SW Avalon (m = 1 SDMNH); Big Fisherman's Cove (m = 1 MVZ); Bulrush Canyon (m = 7 SBMNH; e = 4); Campo Blanco Canyon, below El Rancho Escondido (e = 1); Catalina Harbor (m = 4 SDMNH); lower Cottonwood Canyon, 100 m below Cottonwood Dam (m = 1 SBMNH); Cottonwood Canyon, 0.7 km E Cottonwood Dam (m = 1 SBMNH); Eagles Nest (m = 12 UCLA); upper Fern Canyon, 1.6 km above jct. Cottonwood Canyon (m = 1 SBMNH; e = 2); bluff above Indian Head Point, 0.6 mi. SW Little Harbor, 450 ft (e = 1); Johnson's Landing (m = 15 LACM); Middle Canyon, 0.25 mi. W Eagles Nest Lodge (m = 1 SBMNH); Middle Canyon, 0.1 km W Eagles Nest (m = 2 SBMNH); Middle Canyon, jct. Middle Ranch Road and Ben Weston Road (m = 1 SBMNH); Middle Canyon, S side Thompson Reservoir, 50 yd E spillway (m = 8 SBMNH; e = 4); Middle Ranch, 1100 ft (m = 5 LACM, 3 SBMNH); Middle Ranch Canyon, slope NNW bunkhouse (e = 1); Middle Ranch Canyon, plant propagation facility, E end Thompson Reservoir (e = 2); Middle Ranch Canyon, lower end Thompson Dam (m = 1 SBMNH); White's Landing (m = 10 LACM).

**Locality 3 (PTMUGU;** m = **50, e = 20).** Ventura Co.: Ormond Beach (m = 23 LACM); Pt. Mugu (m = 4 LACM); Pt. Mugu salt marsh (m = 3 LACM); Pt. Mugu Naval Air Station, Beach Road along Dirt Pole Line Road (m = 1 SBMNH; e = 1); Pt. Mugu Naval Air Station, *Salicornia* marsh NW Bldg. 736 to W of S 6th St (m = 2 LACM; e = 2); Pt. Mugu Naval Air Station, *Salicornia* marsh between bldgs. 735 and 738 (m = 8 SBMNH, 1 LACM; e = 9); Pt. Mugu Naval Air Station, end Tacan Road (m = 8 SBMNH; e = 8).

**Locality 4 (DELREY; m = 11,** e = **15).** Los Angeles Co.: Ballona Wetlands (e = 15); Del Rey (m = 2 SDMNH); Playa del Rey salt marsh (m = 8 LACM, 1 UCLA).

**Locality 5 (ANAHEM; m = 17,** e = **15).** Orange Co.: Anaheim Bay salt marsh (m = 2 LACM); Seal Beach National Wildlife Refuge *Salicornia* marsh (m = 8 LACM, 7 SBMNH; e = 15).

**Locality 6 (NEWPRT; m = 12,** e = **11).** Orange Co.: Newport Bay (m = 1 SDMNH); Upper Newport Bay Ecological Reserve (m = 6 LACM, 5 SBMNH; e = 11).

**Locality 7 (STYNEZ; m = 19, e = 18).** Santa Barbara Co.: mouth Santa Ynez River, salt marsh (m = 9 LACM, 10 SBMNH; e = 18).

**Locality 8 (NSBARB;** m = **25, e = 14).** Santa Barbara Co.: Bixby Ranch, ocean bluff adj. Black Canyon, approx. 1 mi. N Pt. Conception (e = 4); Bixby Ranch, jct. Government Point and Point Conception roads, approx. 1 mi. E Pt. Conception (e = 5); Canada del Cojo (m = 2 SBNMH); ¼ mi. W Government Point (e = 1); 1.5 mi. N La Purisima

Mission, 600 ft (m = 3 MVZ); La Purisima Mission, 3.4 mi. NNE Lompoc (e = 3); Los Alamos, Las Flores Ranch (m = 1 SBMNH); Pt. Arguello (m = 7 LACM); N Vandenberg Air Force Base, adj. S20, 1 mi. SW jct. Hwy 1 (m = 2 SBMNH); S Vandenberg Air Force Base (m = 8 SDMNH); S Vandenberg Air Force Base, S jct. Old Coast Road and SLC-4 Road, near Spring Canyon (m = 1 SBMNH; e = 1); S Vandenberg Air Force Base, N side Red Roof Canyon, 0.1 mi. E jct. Coast Road (m = 1 SBMNH).

**Locality 9 (DEVERO; m = 20, e = 13).** Santa Barbara Co.: Devereux Slough (m = 5 LACM, 5 SBMNH, 8 UCSB); Devereux Slough, NW corner (e = 2); Devereux Slough, NE arm adj. horse corrals, Coal Oil Point Reserve (e = 5); Devereux Slough, NE corner below Married Student Housing (e = 1); Devereux Slough, E arm near Devereux School (e = 2); University of California, Santa Barbara, E Side Devereux Slough (e = 3); University of California, Santa Barbara, Stork Campus wetlands (m = 2 UCSB).

**Locality 10 (GOLETA; m = 25, e = 13).** Santa Barbara Co.: Lowlands SW jct. Los Carneros and Mesa roads (m = 6 UCSB); Goleta Slough (m = 1 SBMNH, 18 UCSB; e = 10) University of California, Santa Barbara, Stork Campus W of Los Carneros Road (m = 1 UCSB); University of California, Santa Barbara, Stork Campus SE jct. Los Carneros and Mesa roads (e = 3).

**Locality 11 (SSBARB; m = 29).** Santa Barbara Co.: near Gaviota (m = 6 UCLA); Goleta, middle fork Las Vegas Creek, 1.2 mi. N jct. La Goleta Road (m = 1 UCSB); 0.35 mi. E Greenwell Ave off Via Real (m = 1 SBMNH); near Hendry's Beach, Santa Barbara (m = 1 UCSB); 4.7 mi. N Hwy 101 off Refugio Pass Road (m = 1 SBMNH); Mission Creek along Tunnel Road, 1200 ft (m = 1 SBMNH); Mora Mesa, Central Canyon (m = 1 UCSB); 3 mi. SW Old Mission Santa Barbara (m = 1 SBMNH); Old San Marcos Road, 1 mi. N Cathedral Oaks Road (m = 1 SBMNH); 1 mi. SW Painted Cave area, 1200 ft (m = 1 SBMNH); Santa Barbara, 1166 Palomino Road, 750 ft (m = 11 SBMNH); 5 mi. W Santa Barbara, Hope Ranch (m = 2 UCLA); 4 mi. E Santa Barbara, 600 ft (m = 1 LACM).

**Locality 12 (CARPUP; m = 28, e = 12).** Santa Barbara Co.: Arroyo Paredon, 2 mi. N mouth Carpinteria Slough (e = 12); 2 mi. N Carpinteria (m = 2 UCLA); 2 mi. E by N of Carpinteria (m = 8 MVZ); Carpinteria (m = 2 SDMNH); summit El Rincon Hill (m = 2 LACM); Higgins Ranch, Carpinteria (m = 4 LACM); Santa Ynez Mountains, 3.5 mi. NW Carpinteria (m = 1 LACM); upper Hancock Ranch, Mendoza Canyon (m = 9 LACM).

**Locality 13 (CARPIN; m = 24, e = 14).** Santa Barbara Co.: Carpinteria Marsh (m = 7 LACM, 7 SBMNH; e = 14); El Estero salt marsh, 1 mi. W Carpinteria ( m = 3 LACM, 1 UCSB); Sandyland Dunes, 1.5 mi. W Carpinteria (m = 2 MVZ); Sandyland Slough, Carpinteria (m = 2 MVZ, 2 UCSB).

**Locality 14 (LACOUP; m = 18, e = 11).** Los Angeles Co.: 0.5 mi. NW El Segundo (m = 1 MVZ); Hollywood (m = 1 UCLA); Pasadena (m = 2 UCLA); Puente Hills, near Erras Ranch (m = 1 UCLA); Rancho Palos Verdes, Que Viento Canyon (m = 10 LACM; e = 11); San Dimas (m = 2 UCLA); Santa Monica (m = 1 SDMNH).

**Locality 15 (SCLEMI; m = 14).** Los Angeles Co., San Clemente Island: China Canyon, 200 ft (m = 4 LACM); Horse Beach Cove (m = 8 LACM); Horse Beach Point (m = 1 LACM); Pyramid Cove, salt marsh (m = 1 LACM).

**Locality 16 (ORANGE; m = 20, e = 10).** Orange Co.: Harding Ridge Road, 5 mi. E Tucker Wildlife Sanctuary, 4000 ft (m = 1 LACM); 4.1 mi. N Laguna Beach, Laguna Canyon Road (m = 7 LACM); 15 mi. NE Orange, 450 ft (m = 3 SDMNH); Starr Ranch, Bell Canyon Road (T6S, R7W, Secs. 25 and 36) (m = 6 LACM, 2 SBMNH; e = 9); Trabuco Canyon Road, 2 mi. N, 16 mi. E El Toro (m = 1 LACM; e = 1).

**Locality 17 (SDIEGO; m = 23, e = 7).** San Diego Co.: Oceanside (m = 8 SDMNH); San Onofre (m = 1 SDMNH); mouth Santa Margarita River (m = 4 LACM; e = 7); Santa Margarita area, Camp Pendleton (m = 1 SDMNH); Solano Beach (m = 1 SDMNH); mouth Tijuana River (m = 8 SDMNH).

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# CONTRIBUTIONS IN SCIENCE

## A REVIEW OF THE NATIVE NORTH AMERICAN BEES OF THE GENUS *CHALICODOMA* (HYMENOPTERA: MEGACHILIDAE)

ROY R. SNELLING

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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# A REVIEW OF THE NATIVE NORTH AMERICAN BEES OF THE GENUS CHALICODOMA (HYMENOPTERA: MEGACHILIDAE)

ROY R. SNELLING[1]

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**ABSTRACT.** The five subgenera of *Chalicodoma* known to be present in the Western Hemisphere are separated in a key. The subgenera *Callomegachile, Carinella,* and *Pseudomegachile* are adventive and not treated further. There are two native subgenera. *Chelostomoides,* with about two dozen species, ranges from southern Canada to Peru. The new subgenus *Chelostomoidella* (type-species: *Megachile spinotulata* Mitchell) is monotypic and is limited to arid and semiarid regions of western North America.

The North American species of *Chelostomoides* are separated in a key, and pertinent features of each species are illustrated. Previously treated as a synonym of *C. occidentalis, C. prosopidis* is recognized as a valid species in the United States and northern Mexico; *C. occidentalis* is limited to Lower California, Mexico. The following NEW SYNONYMY is proposed: *C ignacensis* = *C. occidentalis; C. wilmingtoni* = *C. campanulae; C. gualanensis* = *C. abacula; C. exilis* var. *parexilis* = *C. exilis;* and *C. subspinotulata* = *C. spinotulata.*

The following new species are described: *C. axyx* (Costa Rica), *C. alucaba* (Mexico), *C. asymmetrica* (Mexico), *C. ecplectica* (Mexico), and *C. reflexa* (Mexico).

Distributions and host plant associations of each species are briefly discussed.

## INTRODUCTION

*Chelostomoides* is a native New World subgenus of *Chalicodoma* Lepeletier, 1841, a primarily Old World genus of megachiline bees. Originally described as a genus by Robertson (1901), *Chelostomoides* was treated as a subgenus of *Megachile* Latreille, 1802, by Mitchell (1934, 1937, 1956) and most subsequent authors. However, Michener (1962) reviewed the higher groupings of the nonparasitic megachilines and removed *Chelostomoides* to *Chalicodoma* as a subgenus. The only other native New World group of *Chalicodoma,* as redefined by Michener, was the South American subgenus *Stelodides* Moure, 1953. A further refinement of the New World Megachilini was presented by Mitchell (1980), who recognized seven genera; *Stelodides* was transferred to the genus *Chrysosarus* Mitchell, 1943, leaving *Chelostomoides* as the sole native New World representative of *Chalicodoma.* Three Old World subgenera of *Chalicodoma* are represented in the Caribbean region by adventive species, one of which is now apparently established in southern Florida.

The present study was initiated to update published information on some species of *Chelostomoides,* primarily to establish a few new synonymies and to amplify known distributions of a few species. That very modest intent was soon abandoned with the discovery of several new species. Thus, the new key to the known North American species bears little resemblance to that of Mitchell (1956).

## SPECIMENS EXAMINED

During this study, specimens from the following collections have been examined.

Arizona State University (ARSU)
Bee Biology and Systematics Laboratory, USDA, Logan, Utah (BBSL)
California Academy of Sciences (CAS)
California Department of Food and Agriculture (CDFA)
K.W. Cooper, personal collection (KWC)
Florida State Collection of Arthropods (FSCA)
J.A. Halstead, personal collection (HALS)
Museum of Comparative Zoology (MCZ)

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[1] Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

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Natural History Museum of Los Angeles County (LACM)
J.L. Neff, personal collection (NEFF)
San Diego Natural History Museum (SDM)
G.I. Stage, personal collection (GIS)
Texas A&M University (TAMU)
United States National Museum of Natural History (USNM)
University of Arizona (UNAR)
University of California, Berkeley (UCB)
University of California, Davis (UCD)
University of California, Riverside (UCR)
University of Kansas (UKAN)
Washington State University (WASH)

## SPECIMEN DATA

New data on distribution, capture dates, and plant associations are fully cited for those species for which there are few published records. Localities are organized by country, from north to south, and alphabetically by state, province, or department within that country. The designation "state," "department," or "province" is omitted to conserve space. Thus, a locality cited under "MEXICO, *PUEBLA*" is from the State of Puebla of Mexico.

For species that are widely distributed and common, thus well known, only general range is indicated.

Such floral data as are presently available, both from previous literature and from new records, are included for all species. These floral records are arranged alphabetically by families and by genera within families. When records are from four or more species within a floral genus, they are cited thus: *Penstemon* (5 spp.). To the extent that it has been feasible to do so, I have cited floral records using current botanical nomenclature. Therefore, the woody species once included in *Dalea* (Fabaceae) are now placed in the related genus *Psorothamnus* and are cited under the latter name.

## TERMINOLOGY

In general, the morphological terminology employed here is conventional within apoid systematics and the Megachilini (Michener, 1944, 1965; Mitchell, 1935, 1980). Mandibular terminology follows Michener and Fraser (1978).

When the last tergum (6) of the female is viewed in profile, there is a strongly sloping basal face and an oblique posterior rim. The juncture of the two is usually more or less evenly curved. In some species a distinct transverse groove is present, and its posterior margin is marked by a raised carina. When the transverse carina is present, the groove is also present. One species does possess a more or less definite groove, but with no evidence of a carina; this species is placed among those that lack a transverse groove. *Only when both modifications are evident is the transverse groove said to be present.*

The male protarsi are often modified, either broad and flat, or more or less widened and with the anterior and posterior margins curled inward so that the glabrous inner surface appears to be longitudinally grooved. Most species with the latter type of basitarsus possess a unique feature that I have not seen elsewhere among the Megachilini. A cluster of several exceptionally long setae arises at the extreme base of the posterior margin of the basitarsus. The setae are closely appressed to one another for most of their lengths but become separate near their apices; thus, they have the appearance of a single, very long seta, plumose at the apex (Fig. 23). Because of its appearance, I have termed this cluster of setae the *mastigion,* the Greek word for a scourge or whip. In repose, the mastigion commonly lies prostrate along the posterior margin of the probasitarsus, but it may be deflected nearly at right angles to the segment.

The measurements used in the descriptions are those usual to bee systematics and require little explanation beyond that given here.

Head length (HL) is measured with the head in full frontal view and does not include either the labrum or the mandibles; it is measured from the visible dorsal (upper) margin of the vertex to the ventral (apical) margin of the clypeus, including any protuberances of the clypeal margin.

Lower interorbital distance (LID) is the minimum distance between the inner eye margins.

Upper interorbital distance (UID) is the maximum distance between the inner eye margins, usually at about the level of the ocelli.

Flagellar segments are measured along their minimum length.

Wing length (WL) is measured along the costa, from the margin of the tegula to a point opposite the apex of the wing.

## SYSTEMATICS

*Chalicodoma* is used here as defined by Michener (1962): "Mandible of female without cutting edges between teeth (except in *Chelostomoda,* which has one in second interspace only); metasoma strongly convex dorsally, more or less parallel-sided; metanotum separated from propodeum by a suture which is often as conspicuous as scutellar-metanotal suture (except in the subgenus *Chelostomoides*); sublaterally metanotum usually but little narrowed; axillar fossa deep, its posterior face usually ascending to strong scutellar crest between fossa and metanotum; eighth metasomal sternum of male with marginal hairs." Additionally, New World *Chalicodoma* usually possess deep postgradular grooves on metasomal terga 2–4, and in males metasomal sterna 4–8 are usually retracted and hidden. The following new key to the subgenera of *Chalicodoma* now known to be present in the New World is a modification of that of Mitchell (1980). The adventive subgenera *Callomegachile, Carinella,* and *Pseudomegachile* are not further treated here.

## KEY TO NEW WORLD SUBGENERA OF *CHALICODOMA*

1a. Male; antenna 13-segmented; scopa absent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
b. Female; antenna 12-segmented; scopa present on metasomal sterna . . . . . . . . . . . . . . . . . . 6
2a. Metasoma with three exposed sterna; basal metasomal terga without fulvous pubescence or tomentum . . . . . . . . . . . . . . . . . . . . . . . 3
b. Metasoma with four exposed sterna; at least first two metasomal terga with fulvous pilosity . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
3a. Ventral margin of mandible simple (Fig. 15) or with triangular process (Fig. 18) at about midlength; procoxa conspicuously pilose beneath, simple, or with more or less spine-like distal process . . . . . . . . . . . . . . . . *Chelostomoides*
b. Ventral margin of mandible with large basal process (Fig. 17); procoxa glabrous beneath and with both proximal and distal spine-like processes . . . . . . . . . . . . . . *Chelostomoidella*
4a. Protarsus slender and unmodified, probasitarsus pilose on inner surface; fifth and sixth metasomal terga without fulvous pilosity . . . . . . 5
b. Protarsus dilated, probasitarsus with glabrous excavation along anterior, inner margin; fifth and sixth metasomal terga with fulvous pilosity . . . . . . . . . . . . . . . . . . . . . . . . *Callomegachile*
5a. Metasomal terga 3–5 with complete, white, apical pubescent fasciae; lower margin of mandible with small process before middle; gena without posterior marginal carina . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Pseudomegachile*
b. Metasomal terga without fasciae of white pubescence; lower margin of mandible simple; gena with posterior carina . . . . . . . *Carinella*
6a. Without fulvous pubescence on head, mesosoma, and basal terga; mandible various, but often elongate and slender, clypeus often grotesque . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
b. Fulvous pubescence present at least on head, mesosoma, and first two metasomal terga; mandible always broadly triangular, clypeus never grotesque . . . . . . . . . . . . . . . . . . . . . 8
7a. Tergum 6 without preapical groove or, if present, basal face does not project over groove; mandible often long and slender and clypeus often grotesque; mandibular trimma flat, not covered by transparent lamella . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Chelostomoides*
b. Tergum 6 with deep preapical groove and basal face projecting over groove; mandible triangular and clypeus with apical excavation and median tubercle; mandibular trimma with basal depression, covered, in part, by transparent lamella . . . . . . . . . . . . . . . . *Chelostomoidella*
8a. Clypeus, in profile, weakly convex from base to apex and disc with a more or less definite median impunctate line; distal metasomal terga without fulvous pilosity . . . . . . . . . . . . . 9
b. Clypeus, in profile, distinctly beveled and disc without traces of median impunctate line; all metasomal terga with fulvous pilosity . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Callomegachile*
9a. Median line of clypeus cariniform; posterior margins of metasomal terga 3–5 without white pubescent fascia . . . . . . . . . . . . . . . . *Carinella*
b. Median line of clypeus smooth and impunctate but not cariniform; metasomal terga 3–5 with fascia of white pubescence . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Pseudomegachile*

## *Chelostomoides* Robertson

*Chelostomoides* Robertson, 1902:231. Type-species: (*Megachile rufimanus* Robertson, 1891) = *Chelostoma rugifrons* F. Smith, 1854. Monobasic and original designation.
*Oligotropus* Robertson, 1903:168. Type-species: *Oligotropus campanulae* Robertson, 1903. Monobasic and original designation.
*Gnathodon* Robertson, 1903:168. *Preoccupied.* Type-species: *Megachile georgica* Cresson, 1878. Monobasic and original designation.
*Sarogaster* Robertson, 1918:92. New name for *Gnathodon* Robertson, 1903.
*Megachile* subg. *Chelostomoides:* Mitchell, 1934: 306, 309. Mitchell, 1937:382. Michener, 1944: 266, 267.
*Chalicodoma* subg. *Chelostomoides:* Michener, 1962:20. Michener, 1965:193–195. Mitchell, 1980:13, 30–39.

The subgenus *Chelostomoides* is here recharacterized to provide a comparison with the new subgenus *Chelostomoidella,* described below.

### DIAGNOSIS

Differs from *Chelostomoidella,* the only other native North American subgenus of *Chalicodoma,* by the following combination of characters: trimma of mandible flat, without overlying transparent lamella; mandible of male with ventral process, when present, at or beyond midlength; procoxa of male pubescent, ventral process, when present, at apex only; male mesosternum simple; female mandible with outer ridge and secondary ridge low and indistinct; female sternum 6 without preapical groove or, if present, basal face does not overhang groove in profile view.

### DESCRIPTION

**FEMALE.** [1] Mandible long and slender, or short and broad; apical margin with three or four teeth, rarely with five teeth; outer ridge weak to moderate, often evanescent or interrupted beyond proximal one-third, secondary ridge weak beyond basal one-third and interspace broad and shallow, or (in long-mandible species) both ridges essentially absent; trimma flat, without overlying transparent, prostrate lamella. [2] Clypeus flat to moderately convex, rarely strongly convex at base, apical margin usually overhanging base of labrum (if not, disc is bizarrely modified) and simple or variously emarginate, denticulate, or tuberculate. [3] First flagellar segment shorter than second. [4] Lower genal area simple or with small tubercle behind base of mandible.

[5] Meso- and metabasitarsi shorter and narrower than corresponding tibiae; tarsal claws simple or obscurely dentate near base.

[6] Metasoma parallel-sided; tergum 6 without preapical groove or preapical groove present and followed by transverse carina.

**MALE.** [7] Mandible broad to slender, tridentate, inner tooth usually larger than middle tooth, and usually perpendicular to outer margin; process of ventral margin, when present, at or beyond midlength; trimma flat, without overlying transparent lamella. [8] First flagellar segment shorter than second.

[9] Procoxa pubescent or sparsely setose beneath; spine-like process, when present, distal. [10] First three protarsal segments simple or, when modified, without deep channel-like groove on anterior margins of first two segments. [11] Meso- and metabasitarsi shorter and narrower than corresponding tibiae; tarsal claws symmetrical.

[12] Preapical carina of tergum 6 shallowly emarginate, or short-bidentate; lateral and, especially, submedian teeth of posterior margin often low and convex. [13] Sternum 3 without median row of setae simulating a carina. [14] Sternum 4 usually fully retracted, simple. [15] Sternum 5 with species-characteristic patterns of bizarre setae; metasternite not extended over portions of presternite. [16] Sternum 6 with various species-characteristic patterns of bizarre setae; poststernite much shorter than median length of metasternite, apical margin usually transverse. [17] Gonocoxite various, but usually cylindrical or subcapitate distad, rarely compressed. [18] Outer lobe of volsella various, but not notably long and slender. [19] Aedeagus usually ending at same level as gonocoxite, or shorter, normally uniformly pigmented.

## DISCUSSION

For the differences between *Chelostomoides* and *Chelostomoidella*, see the discussion under *Chelostomoidella*. These two are the only native North American subgenera of *Chalicodoma*. One species of *Chalicodoma* is adventive in the United States from India: *C.* (*Pseudomegachile*) *lanata* (Fabricius). Both sexes of that bee have abundant fulvous pubescence on the head, mesosoma, and first two terga; the male, in addition, has four exposed abdominal sterna. This species is known in the United States only from Florida, presumably introduced from Cuba (Hurd, 1979).

Michener (1965) has discussed the many similarities between *Chelostomoides* and the Australian subgenus *Hackeriapis* and expressed the opinion that further study may necessitate combining the two groups. Because I have not had the opportunity to examine many of the Australian forms, I can add no further comment.

Stephen, Bohart, and Torchio (1969) proposed to treat *Chelostomoides* as a genus "... not particularly closely related to *Chalicodoma.*" Because they stated that the range of *Chelostomoides* includes Eurasia as well as the New World, presumably their interpretation includes at least some of the Old World species presently assigned to *Hackeriapis.* The primary justification for this proposal apparently is the modified and concealed fourth sternum of male *Chelostomoides.*

The character of sternum 4 of the males cannot, of itself, be adequate justification for removal of *Chelostomoides* from *Chalicodoma,* and no other supporting characteristics were cited. It should be noted that some *Chelostomoides* (e.g., *C. davidsoni, C. prosopidis, C. occidentalis*) have sternum 4 incompletely concealed. Nor do all species possess specialized, capitate hairs on sternum 5. Although Michener (1965) may well be correct in suggesting that *Hackeriapis* and *Chelostomoides* should be combined, it does not follow that generic status is justified for the enlarged *Chelostomoides.*

*Chelostomoides* is a primarily North American group, with most of the species occurring in the southwestern United States and adjacent Mexico. Michener (1954) recorded no species from Panama, although three species do reach Costa Rica. Three species have been previously reported in South America: *C. cartagenesis* (Mitchell, 1930) (Colombia), *C. haematoxylonae* (Mitchell, 1930) (Colombia), and *C. peruviana* (F. Smith, 1879) (Peru). I have not examined material of any of these species, and they are not dealt with further in this paper; all are included in the key to species of *Chelostomoides* by Mitchell (1956).

Females of *Chelostomoides* often have the clypeus and mandibles grotesquely modified. Although it has been generally assumed that these are adaptive traits, there has never been any observational evidence to bolster the assumption. The observation recently published by Messer (1984), although made on the Indonesian *Chalicodoma pluto* (F. Smith), may very well be applicable to species of *Chelostomoides:* "Facing upward, a female loosened resin with the mandibles, then scraped it up using the elongate labrum in the manner of a bulldozer blade. The ball of resin which formed was held in place between the tree and the labrum while being progressively enlarged ... the labrum was [also] observed to act as a lever, applying tension to a load in the mandibles and possibly helping to secure it during flight."

The species of *Chelostomoides,* so far as known, also use plant resin in nest construction. It seems probable that the clypeal and mandibular modifications may be similarly employed. Because some species of *Chelostomoides* do possess normal, stout mandibles and an essentially simply clypeus, the method of gathering resin may be different.

## KEY TO NORTH AMERICAN *CHELOSTOMOIDES*

1a. Male, antenna 13-segmented and metasoma with three exposed sterna, scopa absent . . 2

b. Female, antenna 12-segmented and metasoma with five exposed sterna, scopa present . . 25

2a. *Either:* (a) ventral margin of mandible without triangular process *or* (b) protarsi flat and broad or expanded and curled with inner surface concave and without pilosity . . . . . . . . . . . 3

b. Ventral margin of mandible with small triangular process at midlength *and* protarsi slender and simple with inner surface densely hirsute . . . . . . . . . . . . . . . . . . . . *armaticeps* (Cresson)

3a. Ventral margin of mandible without tooth or protuberance (Fig. 15); procoxa without distal spine or process on ventral surface; protarsus not flattened and expanded, not excavated beneath . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

b. Ventral margin of mandible with large tooth or protuberance, often hidden by dense hairs (Fig. 18); procoxa commonly with ventral process or spine distad; two or more protarsal segments commonly flattened and broadened, often excavated beneath . . . . . . . . . . . . . . 15

4a. Carina of tergum 6 either bidentate or bilobate, not narrowly protuberant (Figs. 4–8, 11, 12); clypeus and frons usually dull and contiguously punctate, but if punctures are distinctly separated, puncture diameter on basal half of clypeus exceeds 0.035 mm . . . . . . . . . . . . . 5

b. Carina of tergum 6 narrowly protuberant in middle and with apex bidentate (Fig. 9); clypeus and frons shiny between fine, dense punctures, those of clypeus less than 0.03 mm in diameter . . . . . . . . . . *lobatifrons* (Cockerell)

5a. Lateral angles of middle lobe of clypeus tuberculiform or dentiform, emargination between them with median tooth (Fig. 1); carina of tergum 6 low and inconspicuous, weakly emarginate in middle (Fig. 4); apical margin of tergum 6 without lateral or submedian lobes or processes . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

b. Lateral angles of middle lobe of clypeus low and broadly rounded, emargination between them broad and shallow, without median tooth (Figs. 2, 3); carina of tergum 6 commonly bidentate, but if low and inconspicuous, at least lateral teeth evident on apical margin . . . . 8

6a. Clypeus with conspicuous black hairs interspersed among dense white hairs; terga 4 and 5 commonly densely tomentose (often abraded); median tubercle of clypeal margin subequal to, or larger than, flanking tubercles (Fig. 1) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7

b. Clypeus without interspersed black hairs; terga 4 and 5 with only scattered tomentum on discs; median tubercle of clypeal margin conspicuously smaller than flanking tubercles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *manni* (Mitchell)

7a. Middle process of clypeal margin about as long as lateral processes; mandible without tooth-like process below third tooth (Fig. 14); long, black hairs conspicuous on clypeus, frons, and vertex . . . . . . . . . . . . . . . . *abacula* (Cresson)

b. Middle process of clypeal margin much more prominent than lateral processes (Fig. 1); mandible with tooth-like process below third tooth on inner side (Fig. 20); black hairs inconspicuous on clypeus and vertex, absent from frons . . . . . . . . . . . . . . . . . . . . *alucaba,* new species

8a. Carina of tergum 6 conspicuously bidentate (Fig. 11); clypeus and frons shiny between distinctly separated punctures . . . . . . . . . . . . . 9

b. Carina of tergum 6 low and inconspicuous, weakly emarginate or emargination no broader than flanking teeth (Fig. 7, 8); clypeus and frons dull to slightly shiny, contiguously to subcontiguously punctate . . . . . . . . . . . . . . . . . . . 11

9a. Teeth of carina of tergum 6 separated by two or more times their basal width; mesoscutum with distinct anterolateral patch of flocculent white hairs . . . . . . . . . . . . . . . . . . . . . . . . 10

b. Teeth of carina of tergum 6 separated by about their basal widths (Fig. 13); mesoscutum without anterolateral patch of flocculent white hairs . . . . . . . . . . . . . . . . *adelphodonta* (Cockerell)

10a. Clypeus flat, uniformly covered with white hairs; punctures of parapsidal area distinctly separated; ocellocular area with punctures of diverse size and very variable spacing . . . . . . . . . . . . . . . . . . . . . . . . *discorhina* (Cockerell)

b. Clypeus broadly convex over basal one-half or more, hairs white, with interspersed suberect, long, brown to blackish hairs; punctures of parapsidal area contiguous; ocellocular area uniformly subcontiguously punctate, punctures coarser near eye . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *chilopsidis* (Cockerell)

11a. Punctures of vertex about equal to those of mesoscutum; posterior ocelli about as far from eye as from margin of vertex . . . . . . . . . . 12

b. Punctures of vertex distinctly coarser than those of mesoscutum; posterior ocelli distinctly nearer to eyes than to margin of vertex . . . . . . . . . . . . . . . . . . . . . . . . . *rugifrons* (F. Smith)

12a. Frons slightly shiny, punctures contiguous but distinct; mesoscutum with anterolateral patches of flocculent white pubescence; discs of sterna 2 and 3 not tomentose . . . . . . . . . . . . . . . 13

b. Frons dull, rugosopunctate, few punctures distinct; mesoscutum without anterolateral flocculent hair patches; discs of sterna 2 or 3 more or less covered with white tomentum . . . 14

13a. Lateral emarginations of clypeal margin deep, middle portion of margin nearly straight, but depressed in center (Fig. 2); second flagellar segment about four times longer than first, equal to third . . . . . . . . . . *browni* (Mitchell)

b. Lateral and median emarginations of clypeal margin about equal, shallow (Fig. 3); second flagellar segment shorter than third, about three times longer than first . . . . . . . . . . *odontostoma* (Cockerell)

14a. Legs usually wholly ferruginous beyond coxae; pro- and mesobasitarsi each with distinct posterior fringe of very long hairs which are longer than segment (Fig. 25) . . . *axyx,* new species

b. Legs dark brownish, tarsi usually lighter; pro- and mesobasitarsi without posterior fringes, hairs always distinctly shorter than segment (Fig. 26) . . . . . . . . *texensis* (Mitchell)

15a. Protarsal segments broad, flat, and with short, appressed pubescence on outer and inner surfaces . . . . . . . . . . 16

b. Protarsal segments slender or moderately broadened, inner surface of first three segments concave and glabrous . . . . . . . . . . 18

16a. First and second protarsal segments densely tomentose beneath, second with small apubescent area; procoxal process conical, little, if any, longer than wide at base . . . . . . . . 17

b. First protarsal segment with numerous ordinary hairs beneath, not at all tomentose, second segment largely glabrous, with fine tomentum along margins; procoxal process at least twice as long as broad at base . . . . . . . . *georgica* (Cresson)

17a. Distal segment of protarsus much longer than probasitarsus; clypeus with prominent carina-like median ridge, at least near apical margin; ocellocular distance much less than ocelloccipital distance . . . . . . *davidsoni* (Cockerell)

b. Distal segment of protarsus no longer than probasitarsus; clypeus nearly flat, without cariniform median ridge; ocellocular distance about equal to ocelloccipital distance . . . . . . *occidentalis* (W. Fox) and *prosopidis* (Cockerell)

18a. Probasitarsus with short row of slender, apically recurved setae on anteroventral margin; procoxal process prominent . . . . . . . . . . . 19

b. Probasitarsus without apically recurved setae at base of anteroventral margin; procoxal process various, often vestigial . . . . . . . . . . . . 20

19a. Discs of fourth, fifth, and sixth terga with abundant appressed, yellowish pubescence . . . . . . . . . . *otomita* (Cresson)

b. Discs of fourth, fifth, and sixth terga with sparse, mixed short and long, dark, simple hairs only . . . . . . . . . . *reflexa,* new species

20a. Disc of procoxa mostly covered with very short, simple, yellowish to fuscous, decumbent hairs . . . . . . . . . . 21

b. Disc of procoxa mostly covered with long, plumose, white, suberect or erect hairs . . 22

21a. Distal process of procoxa prominent, conoid, usually at least as long as broad at base; pronotal collar with lateral patch of long, flocculent hairs . . . . . . . . . . *subexilis* (Cockerell)

b. Distal process of procoxa short, broader at base than high; pronotal collar without dense patch of flocculent hairs . . . . . . . . . . *angelarum* (Cockerell)

22a. Mastigion present; distal process of procoxa absent or minute; discs of terga 5 and 6 with or without appressed, pale, plumose hairs . . . . . . . . . . 23

b. Mastigion absent; distal process of procoxa distinct, as long as, or longer than, broad at base; discs of terga 5 and 6 with appressed, pale, plumose hairs . . . . . . . . . . *asymmetrica,* new species

23a. Protibia without longitudinal carina on posterior face, or, if present, it is limited to less than distal one-third; disc of procoxa densely tomentose and distal process absent; anterior and posterior margins of probasitarsus divergent distad . . . . . . . . . . 24

b. Protibia with longitudinal carina from near apical spur almost to base; disc of procoxa with well-separated, long, plumose hairs and minute distal process; anterior and posterior margins of probasitarsus subparallel . . . . . . . . . . *campanulae* (Robertson)

24a. Third protarsal segment broader than long and no longer than second segment (Fig. 23); gonocoxite about as broad at midlength as at apex; discs of terga 5 and 6 without appressed, pale, plumose hairs . . . . . . . . . . *exilis* (Cresson)

b. Third protarsal segment longer than broad and longer than second segment (Fig. 24); gonocoxite conspicuously broader at apex than at midlength (Fig. 29); discs of terga 5 and 6 with numerous short, appressed, pale, plumose hairs . . . . . . . . . . *quadridentata* (Mitchell)

25a. Clypeus without erect T-shaped apical process, but may be otherwise modified; supraclypeal area without erect curved process . . . . . . 26

b. Clypeus with erect T-shaped process and supraclypeal area with large curved process (Fig. 75) . . . . . . . . . . *armaticeps* (Cresson)

26a. Tergum 6 with preapical groove; mandible stout, approximately triangular, cutting margin quadridentate and more than one-half as long as lower margin (Figs. 51–53) . . . . . . . . . . 27

b. Tergum 6 without preapical groove; mandible often elongate (Figs. 50, 65), but may be stout and quadridentate as above . . . . . . . . . . 33

27a. Clypeus evenly convex, not bowed across middle, apical margin variously excavated and denticulate or tuberculate . . . . . . . . . . 28

b. Clypeus transversely bowed across middle, lower facet oblique and nearly impunctate, apical margin straight, simple (Fig. 53) . . . . . . . . . . *manni* (Mitchell)

28a. Clypeal margin variously tuberculate or denticulate, but if submedian tubercles are present (one species), margin laterad of tubercles is not concave and tergum 5 lacks apical, pubescent fascia . . . . . . . . . . 29

b. Clypeal margin with strong submedian and lateral tubercles separated by deep emargination;

tergum 5 with apical, pubescent fascia .......................... *subexilis* (Cockerell)

29a. Apical margin of clypeus with deep median emargination flanked by more or less distinct tubercles or denticles (Fig. 51), and without median tubercle .................... 30

b. Apical margin of clypeus with shallow median emargination and median tubercle (Fig. 52) .................................. 31

30a. Tergum 5 without apical fascia of white hairs; punctures of vertex coarse to very coarse (over 0.06 mm diameter), with variable interspaces up to one-half puncture diameter ......... ................ *campanulae* (Robertson)

b. Tergum 5 with apical fascia of white hairs; punctures of vertex moderate (less than 0.055 mm diameter), largely contiguous ......... ................... *angelarum* (Cockerell)

31a. Dorsal pubescence of metasoma whitish, discs of terga 4 and 5 with simple, blackish hairs only .............................. 32

b. Dorsal pubescence of metasoma yellowish to fulvous, discs of terga 4 and 5 with abundant short, appressed, plumose, fulvous hairs .... ...................... *otomita* (Cresson)

32a. Flocculent hairs present at side of pronotal collar and in a more or less defined band across front of mesoscutum; tergum 6 brown pubescent and scopa of sternum 6 largely brownish ........................ *exilis* (Cresson)

b. Flocculent hairs absent, or at least not conspicuously present, laterad on pronotal collar and none across front of mesoscutum; tergum 6 mostly whitish pubescent and scopa of sternum 6 mostly or entirely yellowish ........ ................. *quadridentata* (Mitchell)

33a. Upper face of mandible strongly protuberant at base (Figs. 61, 62, 65, 66, 69, 70) .... 34

b. Upper face of mandible without prominent basal protuberance (Figs. 55, 57, 71) or with low, rounded bulge (Fig. 72) .......... 36

34a. Clypeus with prominent lateral and less prominent median lobe (Figs. 65, 69); labrum without preapical elevation; inner margin of mandible not excavated below basal protuberance .................................. 35

b. Clypeus with sublateral processes that are protuberant at right angles to face (Fig. 60); labrum, in profile, strongly elevated near apex; mandible with deep, pit-like excavation on inner surface below basal protuberance ...... .................. *davidsoni* (Cockerell)

35a. Median clypeal lobe very broad and weakly convex (Fig. 65); mesoscutum with complete anterior fascia of dense, white tomentum .. .................. *lobatifrons* (Cockerell)

b. Median lobe of clypeus narrow and strongly protuberant (Fig. 69); mesoscutum with narrow anterolateral patches of tomentum .... ................... *occidentalis* (W. Fox)

36a. Basal face of tergum 6, in profile, evenly sloping to base of apical lip; clypeus usually convex, apical margin various, but not as below .................................. 37

b. Basal face of tergum 6, abruptly declivitous apicad, forming false preapical groove; clypeus flat, produced in middle, margin of lobe straight and with small apicolateral tubercles (Fig. 55) ................ *adelphodonta* (Cockerell)

37a. Clypeal margin deeply emarginate between two prominent lobes (Figs. 56, 57) ......... 38

b. Clypeal configuration various, but margin not deeply emarginate between prominent lobes .................................. 39

38a. Lobes of clypeus lateral, broadly convex along apical margins (Fig. 57); clypeus flat in middle, supraclypeal area and base of clypeus protuberant in profile ........ *browni* (Mitchell)

b. Lobes of clypeal margin submedian, narrow, acute (Fig. 56); middle of clypeus elevated, supraclypeal area and base of clypeus not protuberant in profile ..................... ............... *odontostoma* (Cockerell)

39a. Mandible short and broad, with four or five teeth, length of apical (dentate) margin much more than one-half length of lower margin (Fig. 71) ............................ 40

b. Mandible long and slender, with three or four teeth, length of apical (dentate) margin always less than one-half and usually less than one-third length of lower margin (Figs. 54, 67) .. .................................. 43

40a. Clypeal margin transverse or slightly produced and irregular or weakly denticulate; mandible with four teeth ...................... 41

b. Clypeus prominently trilobate (Fig. 71); mandible with five teeth .. *prosopidis* (Cockerell)

41a. Clypeus convex, margin produced in middle, with prominent median denticle, irregularly eroded laterad; disc of clypeus with sparse, plumose, white hairs and scattered simple, black hairs ............................ 42

b. Clypeus flattened, margin transverse and irregular; disc of clypeus with sparse, simple, yellowish hairs and a few white, plumose hairs at side ................. *georgica* (Cresson)

42a. Fifth tergum with at least sparse, short, appressed, plumose white hairs along apical margin similar to those on preceding segment, and often with similar hairs on middle of disc; face and vertex with conspicuous, long, blackish hairs ................. *abacula* (Cresson)

b. Fifth tergum without appressed, plumose, white hairs along apical margin or on disc; face with blackish hairs limited to clypeus (usually inconspicuous) and vertex ................. ................... *alucaba*, new species

43a. Middle of clypeus strongly protuberant above and between pair of submedian tubercles on margin (Figs. 54. 67) ................. 44

b. Clypeal configuration not as above, always without developed submedian tubercles on margin (Figs. 59, 73) ................. 45

44a. Legs mostly dark brownish, tarsi lighter; submedian tooth on upper margin of mandible inconspicuous (sometimes absent), margin between it and innermost apical tooth shallowly concave and about as long as apical width of mandibles (Fig. 22) . . . . . . *texensis* (Mitchell)

b. Legs ferruginous (rarely brownish); submedian tooth on upper margin of mandible prominent, margin between it and innermost apical tooth deeply concave and much shorter than apical width of mandible (Fig. 21) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *axyx,* new species

45a. Hypostomal area without cariniform ridge laterad of, and parallel with, hypostomal carina; margins of labrum not evenly convergent apicad; clypeal disc without lateral corni (Figs. 59, 63) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 46

b. Hypostomal area with cariniform ridge laterad of, and parallel with, hypostomal carina; margins or labrum evenly convergent apicad; clypeal disc with lateral corni (Fig. 73) . . . . . . . . . . . . . . . . . . . . . . . . . . . . *ecplectica,* new species

46a. Upper and lower portions of clypeus meeting through a broad, transverse arch (Fig. 63), apical margin simple, without lateral lobes . . 47

b. Clypeus not transversely bowed or arched, median lobe strongly protuberant over basal one-half, lower facet oblique (Fig. 60) . . . . . . . . . . . . . . . . . . . . . . . . . . . *chilopsidis* (Cockerell)

47a. Transverse bow of clypeus broadly interrupted across middle; punctures of vertex very coarse (0.07–0.09 mm), with some interspaces up to one-half puncture diameter . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *rugifrons* (F. Smith)

b. Transverse bow of clypeus continuous across middle (Fig. 63); punctures of vertex moderate (0.03–0.04 mm), uniformly subcontiguous . . . . . . . . . . . . . . . . . . . . *discorhina* (Cockerell)

## Group I (*exilis* Group)

**GROUP CHARACTERS.** Male mandible with ventral triangular process and hypostomal acetabulum present; male protarsal segments concave and glabrous on inner surface; female mandible short and broad, with four or five apical teeth; female clypeal disc unmodified, apical margin more or less denticulate or tuberculate; female tergum 6 with distinct preapical groove.

**INCLUDED SPECIES.** *Chalicodoma angelarum* (Cockerell), *C. asymmetrica,* n. sp., *C. campanulae* (Robertson), *C. exilis* (Cresson), *C. otomita* (Cresson), *C. quadridentata* (Mitchell), *C. reflexa,* n. sp., and *C. subexilis* (Cockerell).

This is the largest species group and the most widely distributed, with species represented from southern Canada to northern South America, but absent from the Hot Desert habitats of western North America. In western North America, species are usually found in montane and submontane areas but intrude into lowland habitats, such as valley floors and prairies, across northern regions. Most species fly during summer months, and nest-provisioning females appear to be highly polylectic.

### *Chalicodoma* (*Chelostomoides*) *angelarum* (Cockerell)

Figure 51

*Megachile angelarum* Cockerell, 1902:70; ♀.
*Megachile* (*Chelostomoides*) *angelarum:* Mitchell, 1937:384, 385, 386–388; ♀♂. Mitchell, 1956:131, 136, 137; ♀♂.

This is one of the most common and generally distributed of the western *Chelostomoides,* ranging from British Columbia to southern California, eastward to Nevada, Arizona, and New Mexico. The range of this species also includes UNITED STATES, *IDAHO:* 2 ♂♂, Wood River, 1 mi NE Gooding Co., 6-7-1980 (M. Wasbauer; CDFA); and MEXICO, *BAJA CALIFORNIA:* 1 ♂, "76.5 km on road to Sierra San Pedro Martir National Park," 20 July 1977 (D. Weismann and C. Mullinex; CAS).

The parasitoid *Sapyga angustata* (Cresson) [Sapygidae] has been reared from nests of *C. angelarum* in California (Linsley, 1944).

This common, widespread species visits a wide variety of flowers, presumably for both pollen and nectar. The following are the known floral records. APIACEAE: *Perideridia gairdneri.* ASTERACEAE: *Achillea millefolium, Aster adscendens, A. canescens, Calycadenia multiglandulosa, Centaurea solstitialis, Chrysopsis fastigiata, C. fremontii, C. villosa, Chrysothamnus* sp., *C. nauseosus, Cirsium* sp., *C. vulgare, Corethrogyne filaginifolia, Encelia farinosa, Erigeron* sp., *Franseria* sp., *Grindelia camporum, G. hallii, Haplopappus arborescens, Helianthus gracilentus, Lessingia leptoclada, Rudbeckia californica, Solidago californica, S. confinis, S. occidentalis.* BORAGINACEAE: *Cryptantha ambigua, C. denticulata, C. intermedia, Heliotropium curassavicum.* BRASSICACEAE: *Brassica* sp., *B. incana, Erysimum asperum.* CAPRIFOLIACEAE: *Lonicera interrupta, Symphoricarpos* sp. FABACEAE: *Amorpha californica, Astragalus douglasii, A. parishii, Cercidium floridum, Glycyrrhiza lepidota, Lathyrus* sp., *Lotus* spp. (13), *Lupinus austromontanus, L. longipes, Medicago sativa, Melilotus alba, M. officionalis, Trifolium variegatum.* FUMARIACEAE: *Dicentra chrysantha.* GENTIANACEAE: *Swertia parryi.* GERANIACEAE: *Geranium richardsonii.* HYDROPHYLLACEAE: *Eriodictyon* sp., *Phacelia* sp., *P. heterophylla, P. imbricata, P. ramosissima.* LAMIACEAE: *Marrubium vulgare, Monardella lanceolata, M. linoides, M. stricta, Salvia apiana, S. pachyphylla, Stachys albens, S. pycnantha, S. rigida, Trichostema larum, T. parishii.* LOASACEAE: *Mentzelia laevicaulis.* ONAGRACEAE: *Clarkia unguiculata, Epilobium angustifolium.* POLEMONIACEAE: *Gilia capitata.* POLYGONACEAE: *Eriogonum* spp. (5). RANUNCULACEAE: *Rhamnus* sp., *R. californicus.* ROSACEAE:

*Harkelia bolanderi* var. *parryi, Potentilla glandulosa*. SAXIFRAGACEAE: *Ribes leucodermis*. SCROPHULARIACEAE: *Collinsia tinctoria, Cordylanthus* spp. (6), *Keckiella* spp. (4), *Penstemon* spp. (5). VERBENACEAE: *Verbena californica, V. prostrata, Vitex* sp.

## ***Chalicodoma* (*Chelostomoides*) *asymmetrica*, new species**

Figures 43–46

### DIAGNOSIS

Male separable from all others possessing a ventral mandibular process, except *C. subexilis*, by the lack of a mastigion on the probasitarsus; differs from *C. subexilis* in having the ventral surface of the procoxa densely covered with abundant plumose white hairs. Female unknown.

### DESCRIPTION

**MALE.** Measurements (mm): Holotype: head width (HW) 2.75; HL 2.23; WL 5.3; total length (TL) 8.1. Paratypes: HW 2.68–2.77; HL 2.18–2.27; WL 5.1–5.2; TL 7.8–8.1.

Head about 1.2 times as broad as long; inner eye margins weakly convergent below, upper interorbital distance about 1.1 times lower interorbital distance; in frontal view, preoccipital margin distinctly elevated above eyes and ocelli. Mandible with prominent ventral process; apex tridentate, inner tooth large, acute. Labrum normal, apex truncate, margins parallel. Clypeus weakly convex; apical margin broadly and weakly incurved, with a small median and a pair of larger submedian tubercles; disc punctures moderate, subcontiguous to contiguous, interspaces shiny; without basal or median impunctate areas. Superclypeal area similar but punctures slightly finer and largely contiguous, hence appearing duller; punctures about as coarse as those of clypeus on vertex and preocciput, becoming subcontiguous, interspaces very weakly tessellate and moderately shiny; gena about half as wide as eye in profile, shiny between subcontiguous moderate punctures that become slightly finer and contiguous near eye margin. Pedicel about twice as long as first flagellar segment, latter broader than long; second flagellar segment about three times longer than first. Interocellar and ocellocular distances subequal and slightly greater than ocelloccipital distance.

Mesoscutum finely tessellate and slightly shiny between subcontiguous to dense moderate punctures; scutellum similar but slightly shinier, punctures contiguous to subcontiguous; metanotum tessellate and slightly shiny between irregularly spaced minute to fine punctures; mesepisternum and metepisternum slightly shiny, punctures moderate and mostly contiguous to subcontiguous, but with irregular interspaces up to a puncture diameter, especially ventrad; side of propodeum slightly shiny between mostly subcontiguous moderate punctures.

Anterior face of procoxa with numerous, long, erect, plumose, white hairs; apical process bluntly triangular, about as long as broad at base. Probasitarsus without mastigion and about three times longer than broad; second segment of protarsus about one-third shorter and about as broad as probasitarsus, asymmetrical; third segment about one-third as long as probasitarsus and narrower than second; all three segments slightly concave on inner face, smooth, shiny, and bare; last protarsal segment distinctly shorter than probasitarsus.

First metasomal tergum shiny between subcontiguous moderate punctures; terga 2–4 shiny, punctures moderate, very variably spaced, from subcontiguous to close; tergum 5 similar but subcontiguously punctate; tergum 6 dull, contiguously finely punctate, carina bilobate, apical margin with low, oblique lateral teeth and broad, lobelike median teeth. Exposed sterna shiny between subcontiguous moderate punctures.

Hidden sterna and genitalia as in Figures 43–46.

Pilosity mostly white and conspicuously plumose; sparse on clypeus except along apical margin; abundant but not wholly concealing surface on rest of face, becoming sparse on vertex-preocciput; pronotum with flocculent hairs only along margin of posterior lobe; mesoscutum without patches or band of flocculent hairs; tergum 1 with flocculent patch on each side of apical margin; terga 2–6 with basal fasciae of short, appressed, plumose hairs, weakest on 2, strongest on 5; disc of terga 5 and 6 uniformly covered with short, plumose, appressed hairs, entirely white on 5 and along midline of 6, yellowish brown on remainder of 6; sterna 1–3 with long, appressed and decumbent, white, plumose hairs, discs of 1 and 2 largely bare, 3 mostly covered but with basolateral bare areas. Clypeus, vertex-preocciput, mesoscutum and scutellum with sparse long, erect, fuscous hairs.

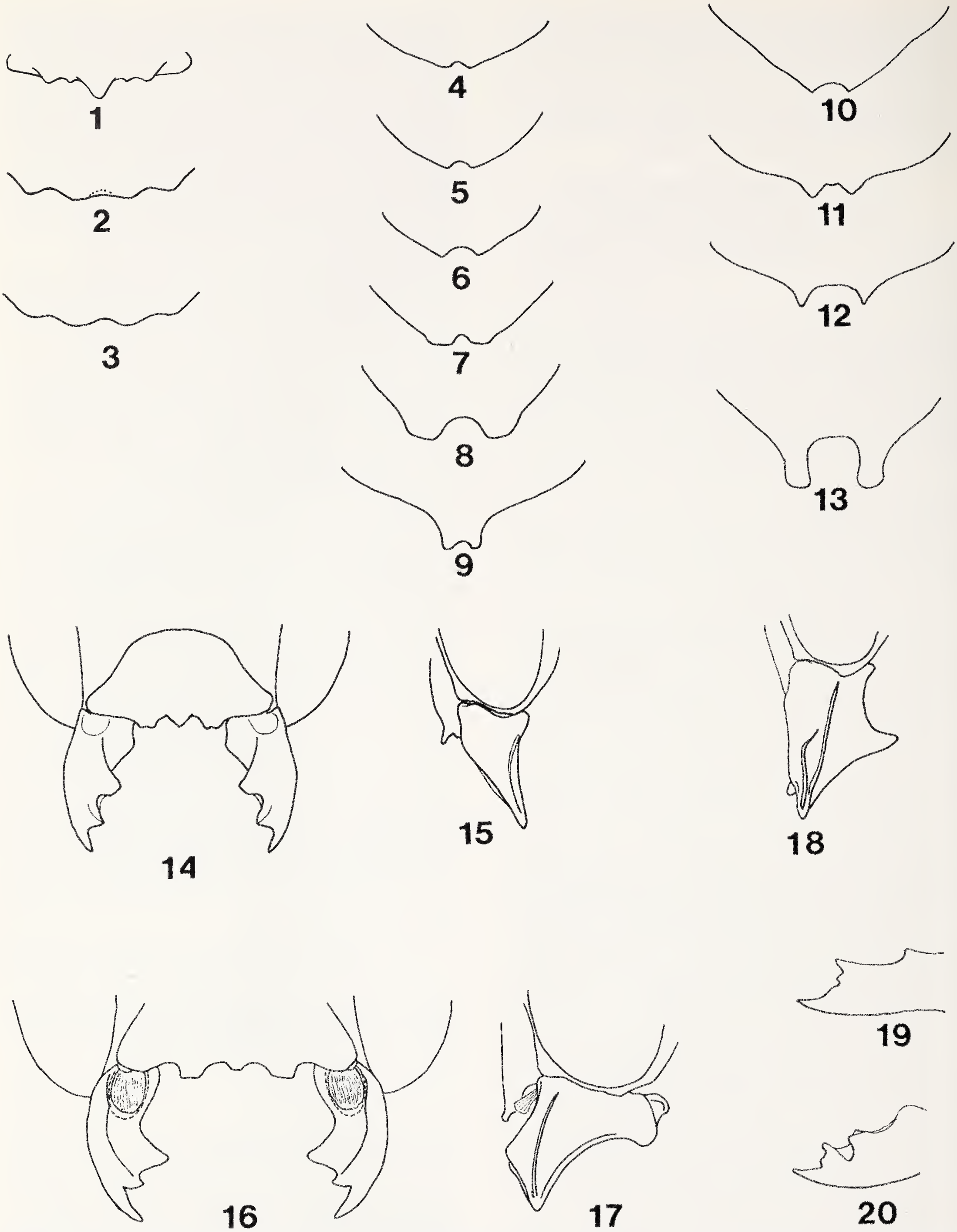
Color mostly blackish brown, becoming lighter on antenna, legs, and metasoma; at least tergum 6, and sometimes margin of tergum 5, somewhat ferruginous. Tegula dark brown. Wings clear, weakly brown, veins and stigma light brown.

### TYPE MATERIAL

Holotype and three paratype males: 17 km W Tehuantepec, *OAXACA*, MEXICO, 8 Sept. 1965 (D.H. Janzen), on *Caesalpinia scelerocarpa* (FABACEAE). Paratypes: 13 ♂♂, Río Chamela, *JALISCO*, 15–24 Apr. 1986 (F.D. Parker); 1 ♂, Puerto Vallarta, *JALISCO*, 25 Jan. 1984 (G.E. Bohart); 2 ♂♂, Kabah, 25 km SW Ticul, *YUCATAN*, 14 Feb. 1987 (C.D.) Michener); 3 ♂♂, Yodzonot, *YUCATAN*, 16 Feb. 1987 (C.D. Michener). Holotype in UKAN; paratypes in LACM, UKAN, and BBSL.

### ETYMOLOGY

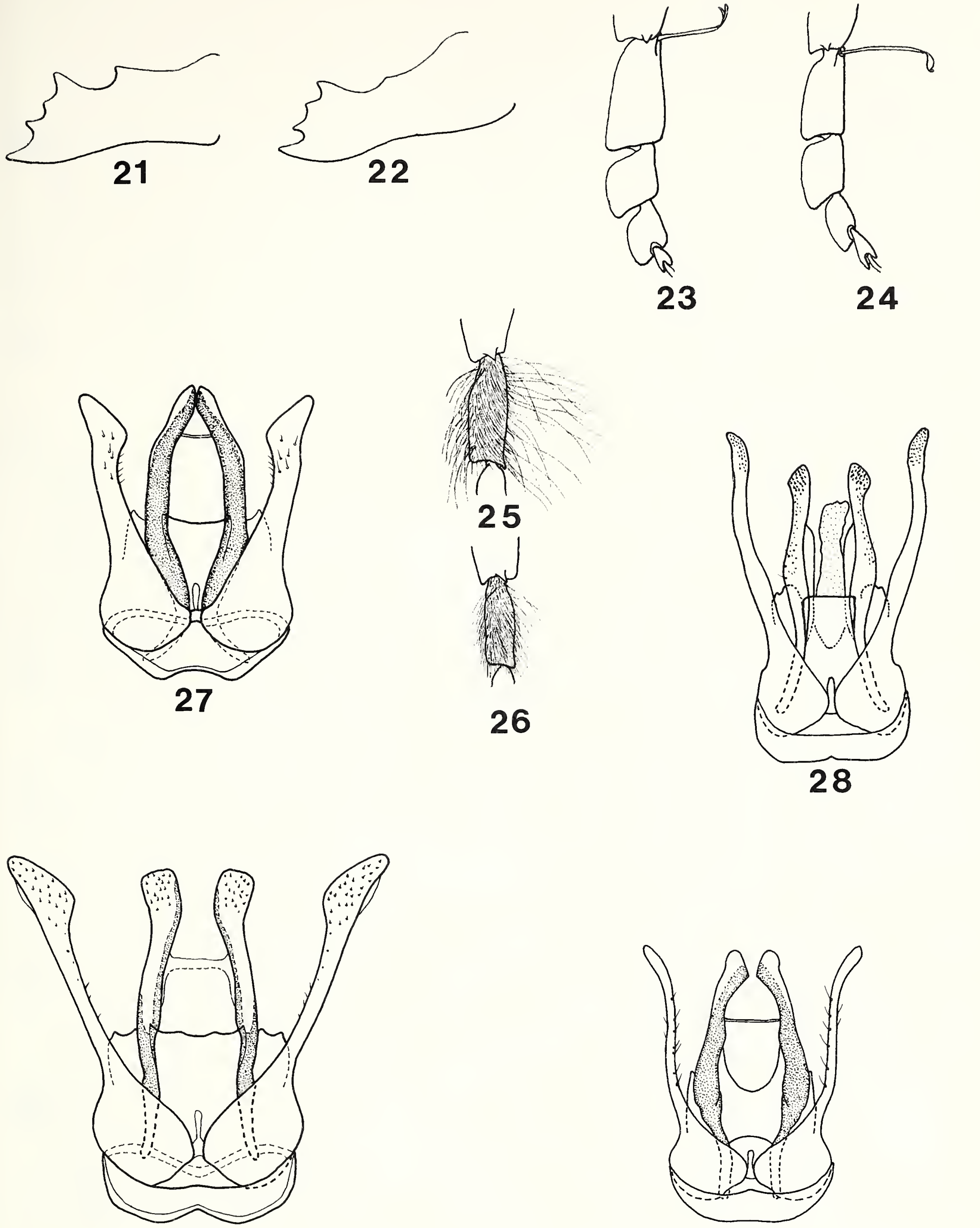
From Greek, *a*- (not) + *symmetros* (equal), in allusion to the shapes of the protarsal segments.



**Figures 1–20.** *Chalicodoma* spp., males. **1–3,** clypeal margin of *C. alucaba* (1), *C. browni* (2), and *C. odontostoma* (3). **4–13,** outline of carina of metasomal tergum 6 of *C. alucaba* (4), *C. browni* (5), *C. odontostoma* (6), *C. davidsoni* (7), *C. reflexa* (8), *C. lobatifrons* (9), *C. texensis* (10), *C. adelphodonta* (11), *C. discorhina* (12), and *C. spinotulata* (13). **14–17,** frontal and lateral views of clypeus and mandible of *C. abacula* (14, 15) and *C. spinotulata* (16, 17). **18,** lateral view of clypeus and mandible of *C. reflexa*. **19, 20,** mandible of *C. axyx* (19) and *C. alucaba* (20).

## DISCUSSION

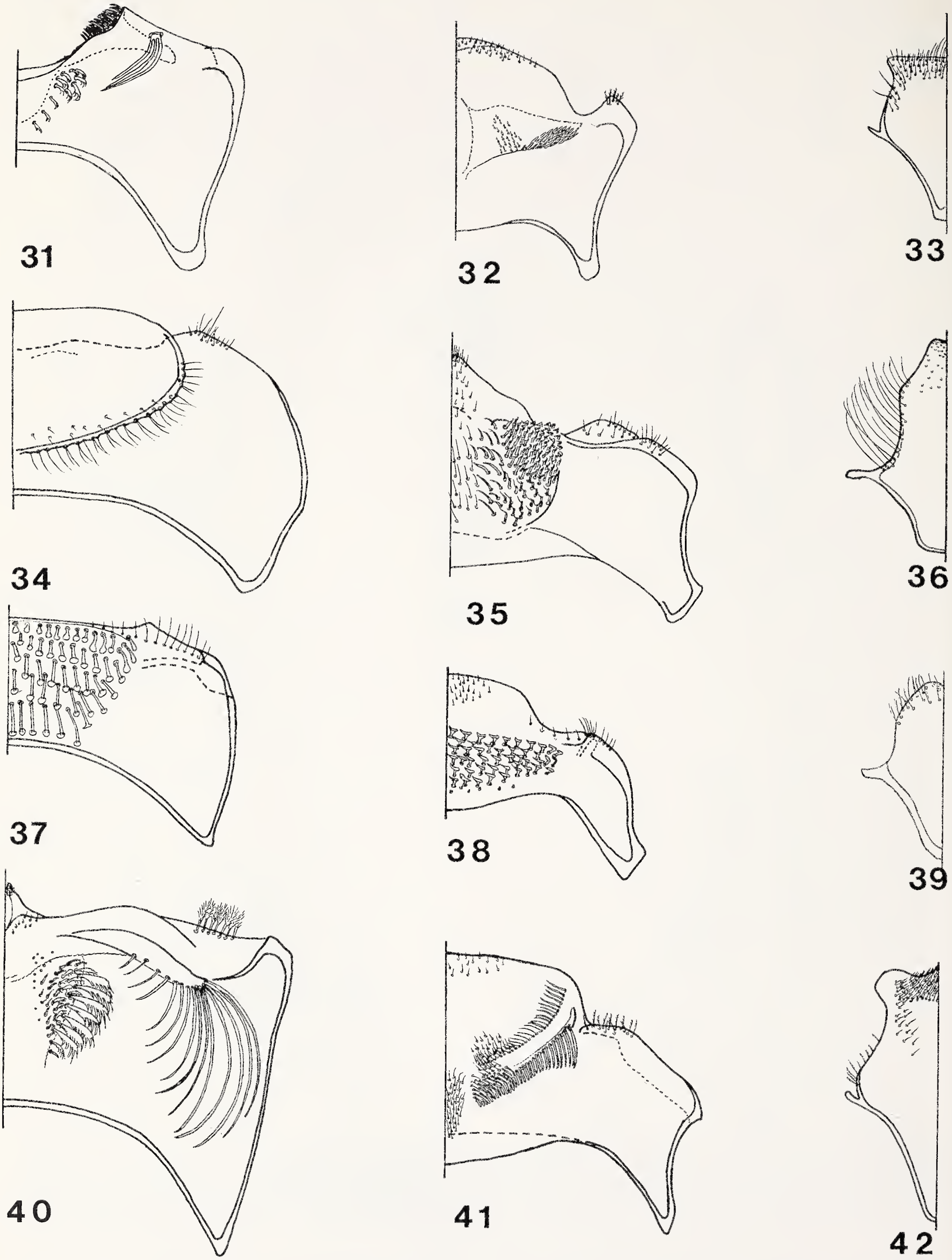
In addition to the above types, one additional male has been seen: 10.7 mi N Ciudad del Valle, 950 ft. elev., San Luis Potosí, MEXICO, 2 Sept. 1962 (University of Kansas Mexico Expedition; UKAN). It is smaller than any in the type series (HW 2.59, HL 2.05, WL 5.1, TL 7.5) but is otherwise very similar to the specimens from Oaxaca, although the disc of sternum 3 is largely bare.



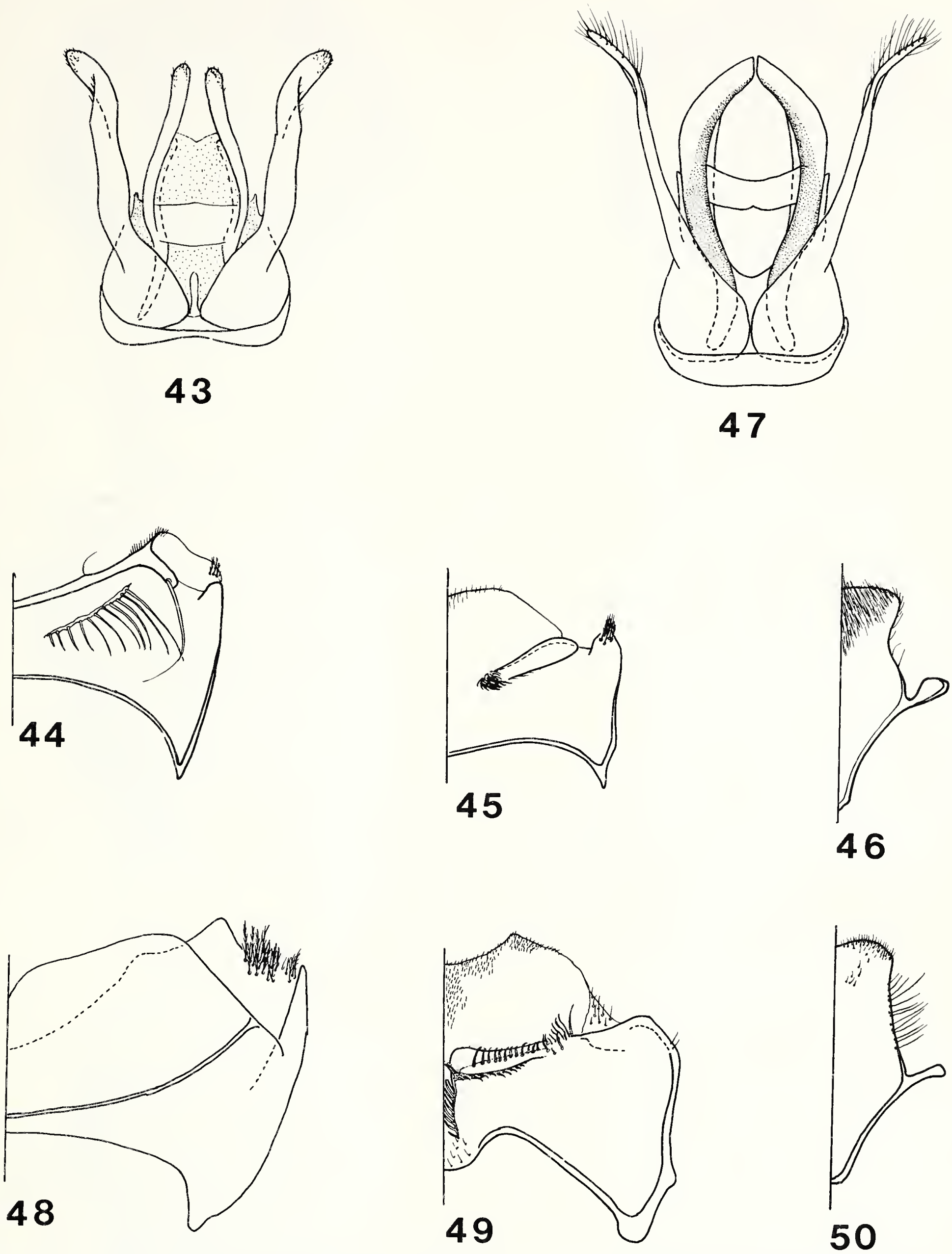
**Figures 21–30.** *Chalicodoma* spp. **21, 22,** mandible of female of *C. axyx* (21) and *C. texensis* (22). **23, 24,** protarsus of male of *C. exilis* (23) and *C. quadridentata* (24). **25, 26,** mesobasitarsus of male of *C. axyx* (25) and *C. texensis* (26). **27–30,** male genitalia, dorsal view, of *C. axyx* (27), *C. quadridentata* (28), *C. reflexa* (29), and *C. alucaba* (30).

Because the probasitarsus lacks a mastigion, this species is readily separable from males of other species that possess a ventral mandibular process, except that of the similar *C. subexilis*. Males of *C. subexilis* have the anterior face of the procoxa covered with short, yellowish, simple bristles, rather than long, erect, plumose, white hairs. In addition, males of *C. subexilis* lack fuscous hairs on the clypeus, the disc of tergum 5 is without appressed, plumose hairs, and the first flagellar segment is about as long as broad ad subequal to the pedicel in length.

A female collected by F.D. Parker at Rio Cha-



**Figures 31–42.** *Chalicodoma* spp., male metasomal sterna 5, 6, and 8, respectively, of *C. quadridentata* (31–33), *C. axyx* (34–36), *C. alucaba* (37–39), and *C. reflexa* (40–42).

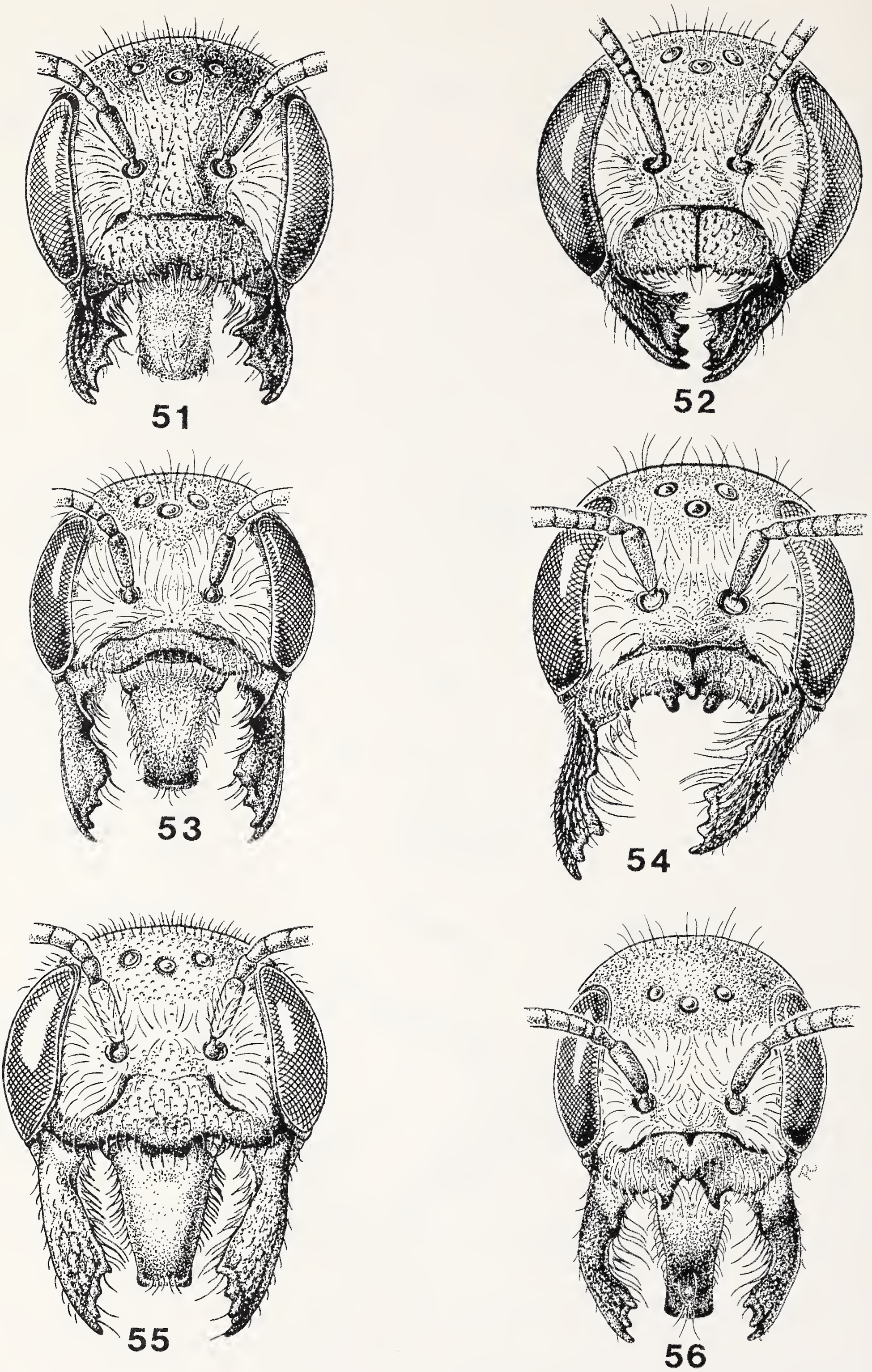


**Figures 43–50.** *Chalicodoma* spp., males, genitalia (dorsal view) and metasomal sterna 5, 6, and 8, respectively, of *C. asymmetrica* (43–46) and *C. spinotulata* (47–50).

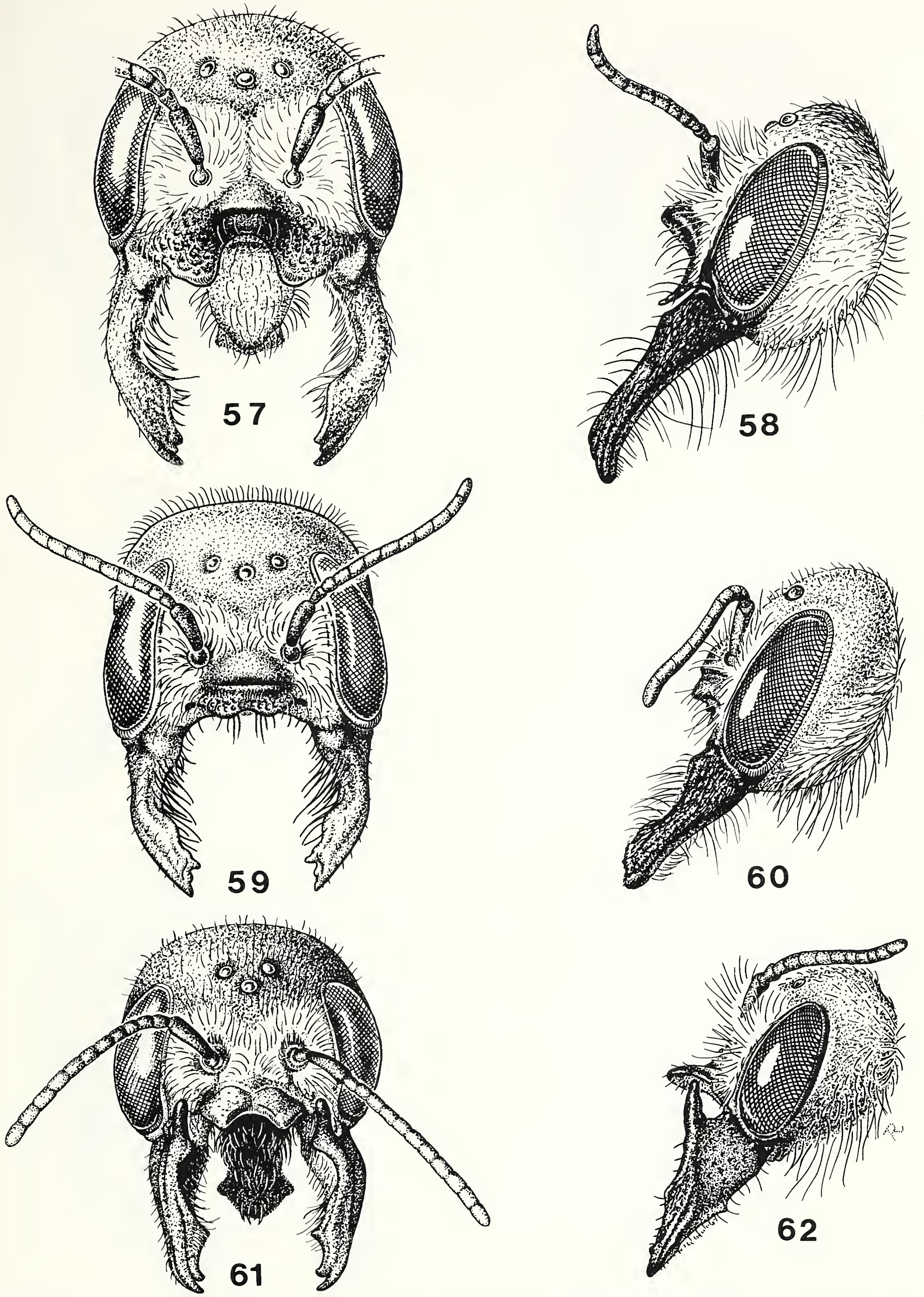
mela probably belongs to this species. Morphologically it is hardly separable from those of *C. quadridentata,* to which it will go in the above key. It is smaller than females of *C. quadridentata,* with the head width only about 2.5 mm, whereas that of *C. quadridentata* exceeds 3.5 mm; metasomal tergum 5 lacks an apical, pubescent band and the discs of 5 and 6 have conspicuous, short, subappressed to appressed, yellowish pubescence.

## *Chalicodoma* (*Chelostomoides*) *campanulae* (Robertson)

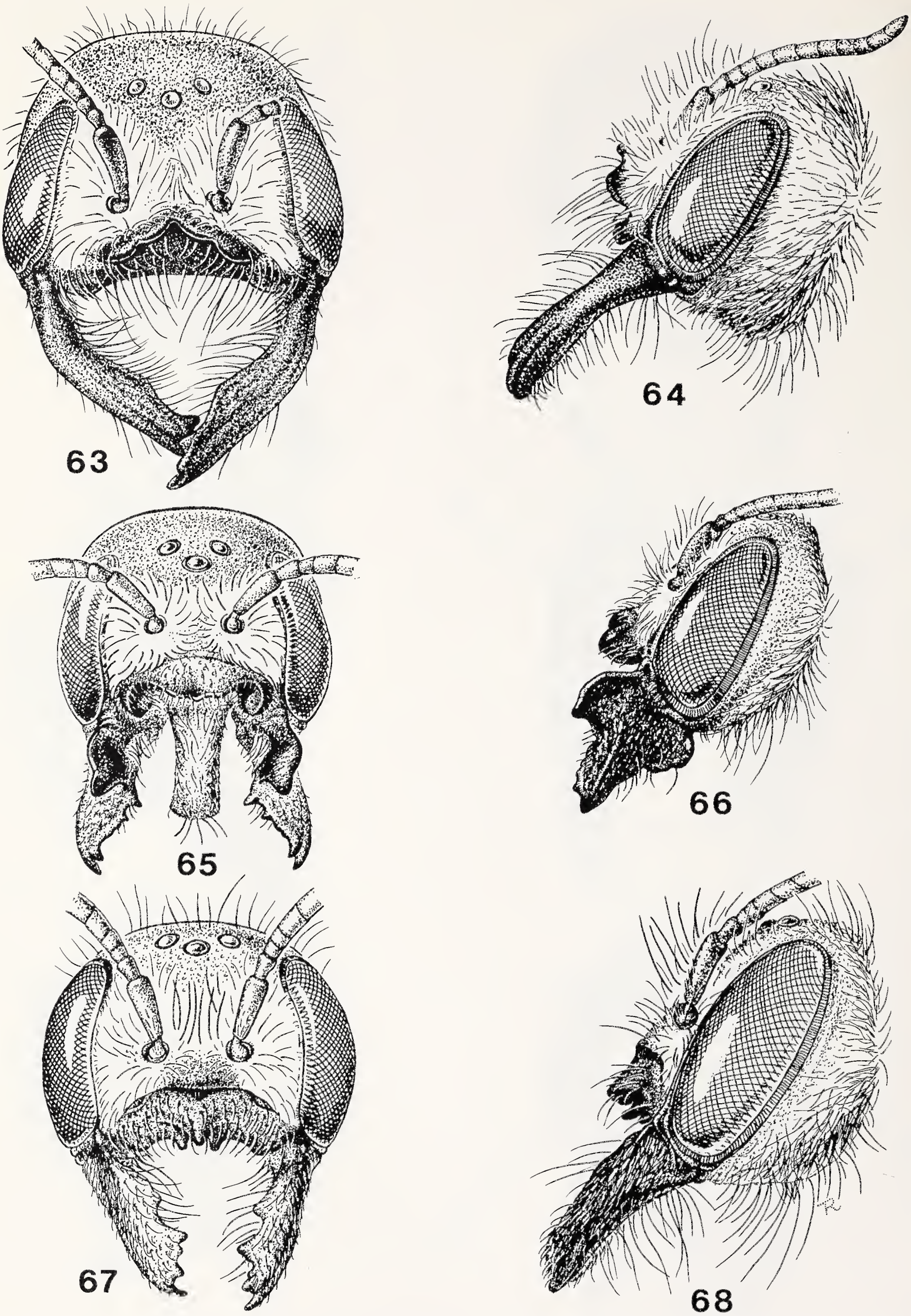
*Oligotropus campanulae* Robertson, 1903:171; ♀♂.
*Oligotropus wilmingtoni* Mitchell, 1924:156; ♀♂. NEW SYNONYMY.
*Megachile* (*Chelostomoides*) *campanulae* var. *wilmingtoni:* Mitchell, 1937: 391; ♀.



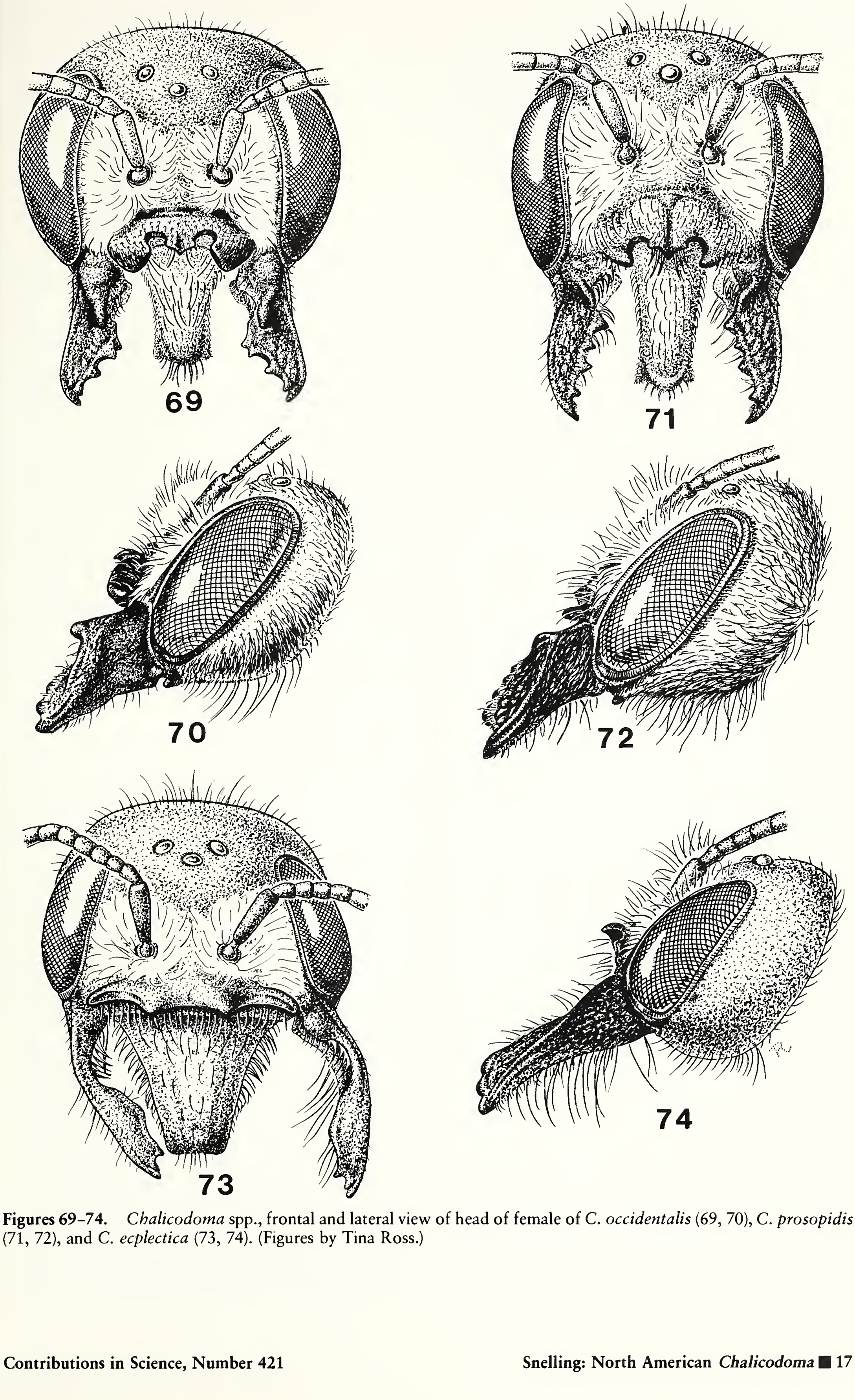
**Figures 51–56.** *Chalicodoma* spp., frontal view of head of female of *C. angelarum* (51), *C. exilis* (52), *C. manni* (53), *C. texensis* (54), *C. adelphodonta* (55), and *C. odontostoma* (56). (Figures by Tina Ross.)



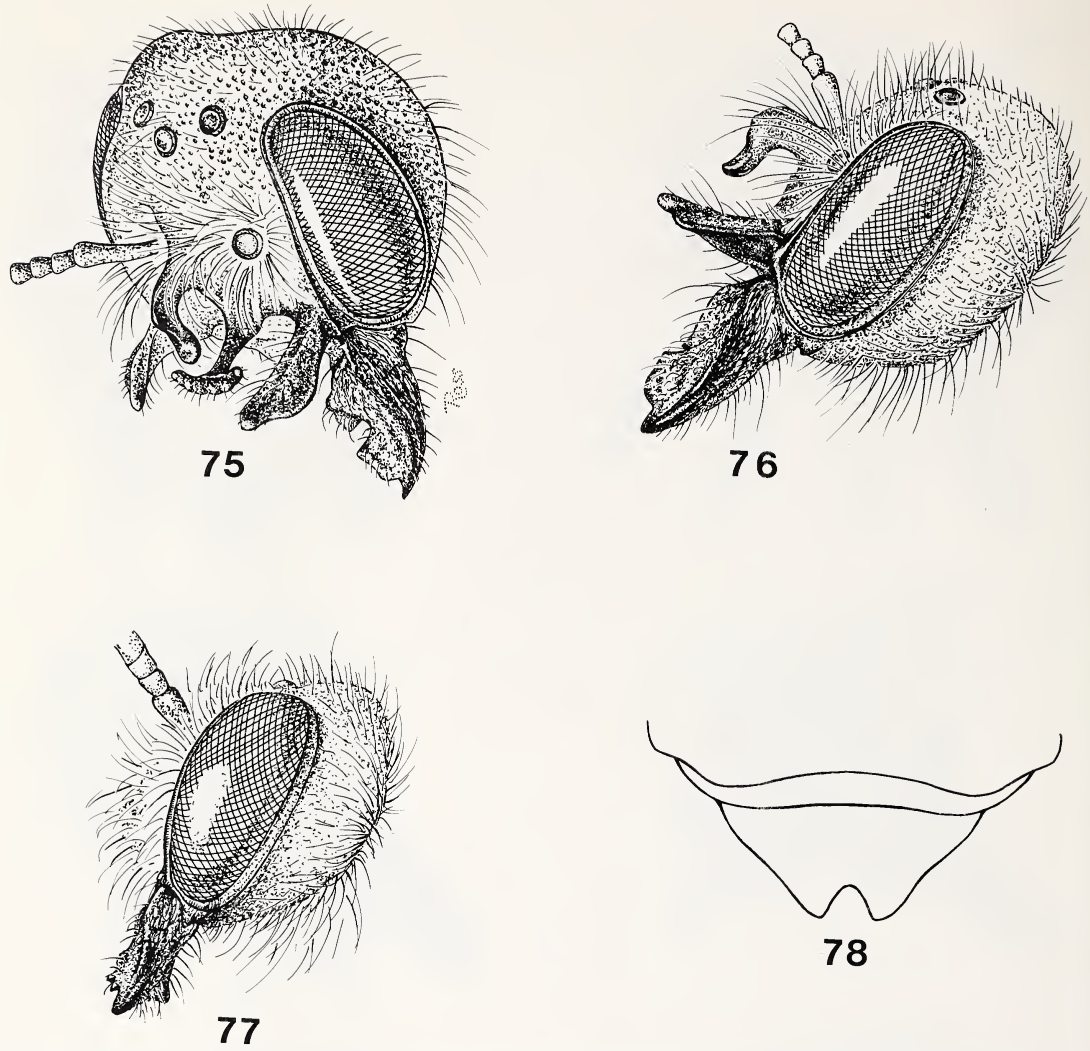
**Figures 57–62.** *Chalicodoma* spp., frontal and lateral view of head of female of *C. browni* (57, 58), *C. chilopsidis* (59, 60), and *C. davidsoni* (61, 62). (Figures by Tina Ross.)



**Figures 63–68.** *Chalicodoma* spp., frontal and lateral view of head of female of *C. discorhina* (63, 64), *C. lobatifrons* (65, 66), and *C. axyx* (67, 68). (Figures by Tina Ross.)



**Figures 69–74.** *Chalicodoma* spp., frontal and lateral view of head of female of *C. occidentalis* (69, 70), *C. prosopidis* (71, 72), and *C. ecplectica* (73, 74). (Figures by Tina Ross.)



**Figures 75–78.** *Chalicodoma armaticeps.* **75, 76,** lateral and oblique views of head of female; **77,** lateral view of male head; and **78,** outline of transverse carina of male metasomal tergum 6. (Figures by Tina Ross.)

The variety or subspecies *wilmingtoni* differs from the typical form in possessing darker wings and black pubescence on the sixth sternum of the female. The range of the variant lies wholly within that of the nominate form, and many specimens of intermediate character have been seen. Variation seems to be clinal, with specimens becoming progressively darker in coastal areas of the Carolinas, Georgia, and Florida. Under the circumstances, there is no justification for formally separating the variant phenotype.

The range of *C. campanulae* extends from Quebec and Massachusetts south to Florida, and into the midwestern United States, from Minnesota to central Texas. The westernmost records are from *COLORADO:* 1 ♀, 5 mi S Coaldale, 7300 ft elev., Fremont Co., 13 Aug. 1969 (C.D. Michener; UKAN); 2 ♂♂, 2 mi S Coaldale, 7500 ft elev., Fremont Co., 10 Aug. 1964 (C.D. Michener; UKAN), on *Campanula. MONTANA:* 1 ♀, near Florence, Ravalli Co., 24 June 1980 (D. Yanega; UKAN).

Nests are constructed in borings in wood; the cleptoparasitic bee, *Coelioxys modesta* F. Smith, has been reared from nests of *C. campanulae* (Krombein, 1967).

Known floral records for *C. campanulae* are as follows. ASCLEPIADACEAE: *Asclepias* sp. ASTERACEAE: *Helianthus* sp., *Rudbeckia* sp., *Solidago* sp. CAMPANULACEAE: *Campanula* sp., *C. americana, C. campanulae, C. rotundifolia.* CAPRIFOLIACEAE: *Symphoricarpos* sp. FABACEAE: *Baptisia tinctoria, Desmodium canadense, Galactia* sp., *Melilotus* sp., *Phaseolus* sp., *Psoralea* sp. LAMIACEAE: *Monarda* sp., *Nepeta* sp., *Pycanthemum* sp. LOBELIACEAE: *Lobelia* sp. LYTHRACEAE: *Lythrum* sp. MALVACEAE: *Malva sylvestris.* ONAGRACEAE: *Epilobium angustifolium, Oenothera* sp. PONTEDERIACEAE: *Ponte-*

*deria* sp. SCROPHULARIACEAE: *Veronica* sp. VERBENACEAE: *Verbena* sp.

## *Chalicodoma* (*Chelostomoides*) *exilis* (Cresson)

Figures 23, 52

*Megachile exilis* Cresson, 1872:265; ♂.
*Megachile studiosa* Cresson, 1872:269; ♀.
*Megachile* (*Chelostomoides*) *exilis* var. *parexilis* Mitchell, 1937:393–394; ♂. NEW SYNONYMY.

The eastern form, variety *parexilis,* was based on male specimens that differed slightly from the nominate, western form in having the third protarsal segment nearly as wide as the second. No female differences were noted. Variation within populations is sufficiently broad that many western males may be assigned to the eastern variant. The eastern form does appear to be generally more consistent, but not wholly so. I see no utility in recognizing those males with a broader third tarsal segment as a separate subspecies.

This species ranges from the mountains of southern Arizona east to the Atlantic coastal states, from Virginia and Maryland south to Florida. The following specimens have been seen from MEXICO. *BAJA CALIFORNIA SUR:* 1 ♂, La Laguna, 1675–1725 m elev., Sierra de La Laguna, 28 Aug.–1 Sept. 1977 (R.R. Snelling; LACM), on *Gnaphalium* sp. *HIDALGO:* 1 ♂, 9 mi S Zimapán, 6100 ft elev., 23 June 1953 (University of Kansas Mexican Expedition; UKAN). *MORELOS:* 1 ♀, 7 mi NE Yautepec, 4000 ft elev., 18 Aug. 1962 (University of Kansas Mexican Expedition; UKAN); 1 ♀, 7.3 mi S Yautepec, 3000 ft elev., 16 Aug. 1962 (Ordway and Naumann; UKAN); 1 ♀, 0.6 km S Teacalco, 1020 m elev., 16 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Crotalaria incana. SAN LUIS POTOSI:* 1 ♀, 3.4 mi NE El Naranjo, 800 ft elev., 5 Sept. 1962 (University of Kansas Mexican Expedition; UKAN). *SONORA:* 1 ♀, Alamos, 7 Sept. 1970 (G.E. and R.M. Bohart; BBSL). *TAMAULIPAS:* 1 ♂, 6.2 mi S San Fernando, 9 July 1966 (University of Kansas Mexican Expedition; UKAN); 1 ♂, 80 km S Ciudad Victoria, 23 June 1981 (B. Miller, C. Porter, and L. Stange; FSCA); 1 ♀, Llera Mesa, 1800 ft elev., 7 June 1961 (University of Kansas Mexican Expedition; UKAN).

This wide-ranging species flies mainly during the summer months, with most records during June, July, and August. There are, however, records as early as March and as late as October.

A wide variety of flowers is visited for nectar and/or pollen, including 32 genera in 13 families, as follows. ANACARDIACEAE: *Rhus* sp. ASCLEPIADACEAE: *Asclepias* sp., ASTERACEAE: *Baccharis* sp., *Bidens pilosa, Coreopsis* sp., *Erigeron* sp., *Gnaphalium* sp. BIGNONIACEAE: *Chilopsis linearis.* BRASSICACEAE: *Sisymbrium linearifolium.* CELASTRACEAE: *Ilex* sp. ERICACEAE: *Vaccinium* sp. FABACEAE: *Baptisia tinctoria, Cracca edwardsii, Crotalaria* sp., *C. incana, Dalea* sp., *Galactia* sp., *Lespedeza repens, Lupinus* sp., *L. texensis, Melilotus* sp., *M. officionalis, Parkinsonia aculeata, Phaseolus* sp., *P. limensis, Sesbania sesbans, Tephrosia virginiana, Trifolium* sp., *Vicia* sp. HYDROPHYLLACEAE: *Hydrolea* sp. LAMIACEAE: *Mentha* sp., *Monarda* sp. ONAGRACEAE: *Oenothera* sp. POLYGALACEAE: *Polygala* sp. RHAMNACEAE: *Ceanothus* sp., *Condalia* sp.

## *Chalicodoma* (*Chelostomoides*) *otomita* (Cresson)

*Megachile otomita* Cresson, 1878:123; ♂. Mitchell, 1930:176.
*Megachile squamosa* Friese, 1916:340–341; ♀♂.
*Megachile knabi* Cockerell, 1919:215; ♂.
*Megachile* (*Chelostomoides*) *otomita:* Mitchell, 1930:158, 170, 176. Mitchell, 1956:135, 138.

Friese (1916) described *M. squamosa* from females from San José, Costa Rica, and a male from Popayan, Colombia. Cockerell's *M. knabi* was described from Cordoba, Mexico. Both names were correctly recognized as synonyms of *M. otomita* by Mitchell (1930), who recorded additional specimens from San José and "Mount Redonda," Costa Rica. Cockerell (1949) recorded specimens of both sexes from Zamorano, Honduras.

The following data will amplify our knowledge of the distribution of *C. otomita.* MEXICO, *CHIAPAS:* 1 ♂, 28 mi W Cintalapa, 9 Apr. 1962 (F.D. Parker; BBSL); 2 ♂♂, El Sumidero, 17 Sept. 1975 (J.L. Neff; NEFF), on composite. *JALISCO:* 2 ♀♀, 1 ♂, Laguna Chapala, 21 Aug. 1957 (A.P. Yerington; LACM); 1 ♂, 24.1 mi NW Tequila, 11 Aug. 1963 (G.W. Byers; UKAN). *MORELOS:* 1 ♀, 6.7 mi W. Yautepec, 29 July 1963 (M. Naumann and A. Wille; UKAN); 1 ♂, 6 mi SW Jonocatepec, 3700 ft elev., 18 Aug. 1962 (University of Kansas Mexican Expedition; UKAN); *OAXACA:* 1 ♂, 2 mi NW Jamiltepec, 12 Oct. 1975 (J.L. Neff; NEFF), on *Salvia;* 1 ♂, 3.4 mi S Jacatepec, 2400 ft elev., 16 July 1973 (R.R. Snelling and T. W. Taylor; LACM); 1 ♂, Oaxaca, 5000–5580 ft elev., 2 May 1965 (H.V. Weems; FSCA), on *Aster;* 1 ♀, 4 mi W Zanatepec, 200 m, 15 Sept. 1975 (J.L. Neff; NEFF), on composite; 1 ♂, 23 mi S Matias Romero, 22 Apr. 1962 (F.D. Parker; BBSL). *QUINTANA ROO:* 2 ♀♀, X-can, 8 May 1963 (E.C. Welling; LACM). *SAN LUIS POTOSI:* 1 ♀, 9 mi S Ciudad del Valle, 600 ft elev., 2 Sept. 1962 (University of Kansas Mexican Expedition; UKAN); 1 ♀, 10.7 mi N Ciudad del Valle, 950 ft elev., 2 Sept. 1962 (University of Kansas Mexican Expedition; UKAN); 2 ♀♀, 9 ♂♂, El Salto, 1700 ft elev., 15 July 1963 (University of Kansas Mexican Expedition; UKAN); 3 ♂♂, same locality and date (G.W. Byers; UKAN); 1 ♂, El Salto, Río Salto, 27 July 1969 (G. Gordh and D. Kamm; UKAN); 2 ♂♂, 7 mi NW Tamazunchale, 15 July 1968 (M.G. Naumann; UKAN). *TAMAULIPAS:* 1 ♀, 1 ♂, 17 mi S Llera, 16 June 1953 (University of

Kansas Mexican Expedition; UKAN); 1 ♂, 6.6 mi W Antiqua Morelos, 400 ft elev., 3 Sept. 1962 (Ordway and Naumann; UKAN). *VERA CRUZ:* 1 ♂, Río Atoyac, 5 mi NW Potrero, 15 July 1973 (R.R. Snelling and T. W. Taylor; LACM); 1 ♀, 9 mi N Tempoal, 6 June 1965 (Burke, Meyer, Schaffner; TAMU). *YUCATAN:* 7 ♀♀, 3 ♂♂, Yodronot, 16 Feb. 1987 (C.D. Michener; UKAN); 2 ♂♂, Uxmal ruins, 16 km SW Muna, 14 Feb. 1987 (C.D. Michener; UKAN). BELIZE, *COROZA:* 2 ♀♀, 15 mi S Santa Elena, 1 July 1966 (University of Kansas Mexican Expedition; UKAN). GUATEMALA: 1 ♀, 6.3 mi NE Esquintla, 30 July 1966 (University of Kansas Mexican Expedition; UKAN). COSTA RICA, *CARTAGO:* 1 ♀, Turrialba, 8 May 1948 (F. Shrader; UKAN). *GUANACASTE:* 6 ♀♀, Liberia, 15–16 Feb. 1972 (P.A. Opler, UCB), on *Andira inermis;* 19 ♀♀, 3 ♂♂, same locality and collector, 23–26 Feb. 1972, on *An. inermis;* 5 ♀♀, same locality and collector, 1 Mar. 1972, on *An. inermis;* 1 ♂, Finca La Pacifica, 4 mi NW Cañas, 19 May 1971 (P.A. Opler; UCB), on *Acacia tenuiflora;* 2 ♀♀, 2 ♂♂, Hacienda Comelco, 24 km NW Cañas, 6 Mar. 1972 (E.R. Heithaus; LACM), on *An. inermis,* 1045–1120 hr; 5 ♀♀, same locality and collector, 9 Mar. 1972, on *An. inermis,* 0745–0815 hr; 1 ♂, Hacienda Comelco, 8 km W Bagaces, 26 Jan. 1972 (P.A. Opler; UCB), on *Triplaris americana;* 1 ♂, same locality and collector, 29 Sept. 1973, on *Lotus;* 2 ♀♀, El Coco, 20 June 1963 (Kerfoot et al.; UKAN); 5 ♀♀, El Coco, 21 June 1963 (C.D. Michener; UKAN). SAN JOSE: 15 ♀♀, Santa Ana, 31 July 1963 (C.D. Michener and O'Conner; UKAN). COLOMBIA, *ANTIOQUIA:* 1 ♀, Río Porce, 1000 m elev., 2 Oct. 1976 (C.D. Michener; UKAN). *VALLE:* 1 ♀, 2 ♂♂, Loboguerrera, 740 m elev., 4 Feb. 1977 (M. Breed and C.D. Michener; UKAN); 1 ♂, Ginebra, 13–14 July 1979 (M.A. Tidwell; FSCA); 1 ♀, Central Hidroelectrica de Anchicaya, 17 Mar. 1979 (J. Monsalve; FSCA); 2 ♀♀, 1 ♂, Atuncela, Nov. and Dec. 1974 (R.C. Wilkerson; FSCA); 16 ♀♀, 34 ♂♂, Finca San Luis, 1010 m elev., Municipio Candelaria, dates throughout 1975 (R.C. Wilkerson; FSCA), all from malaise trap.

The above records include floral genera representing four families. ASTERACEAE: *Aster* sp. FABACEAE: *Acacia tenuiflora, Andira inermis, Lotus* sp. LAMIACEAE: *Salvia* sp. POLYGONACEAE: *Triplaris americana.*

## *Chalicodoma* (*Chelostomoides*) *quadridentata* (Mitchell)

Figures 24, 28, 30–32

*Megachile quadridentata* Mitchell, 1930:177–178; ♀.

This species was described from a single female from Guadalajara, Mexico, and was compared with *C. exilis* and superficially similar species. The type is now in the USNM, and I have examined it. There is no question but that it is very similar to *C. exilis.* Were the status of *C. quadridentata* to be determined from this one specimen, I would have declared it a synonym of *C. exilis.* The differences between the two are not impressive.

Numerous additional females, and associated males, are available. With these at hand, it is apparent that *C. quadridentata* should be treated as a discrete species that maintains its integrity in areas of sympatry with *C. exilis.* Females of *C. quadridentata* do not possess a cluster of flocculent, white hairs at the side of the pronotal collar, as do those of *C. exilis.* Some specimens of *C. exilis* from the southeastern United States are similar but do possess a thin band of flocculent hairs across the front of the mesoscutum. Such hairs are uniformly lacking in females of *C. quadridentata* that I have seen. In particular, there are no flocculent hairs in the vicinity of the notaulices.

The few females of *C. exilis* available from central Mexico are similar to those of *C. quadridentata.* Although flocculent hairs are present on the sides of the pronotal collar, they are less conspicuously plumose than those of females from the United States. Flocculent hairs are generally absent across the front of the mesoscutum, but some are present on the notaulices. In these *C. exilis* females, the sixth tergum is dark pubescent; most females of *C. quadridentata* have conspicuous, pale, plumose hairs, though some (including the type) are dark pubescent.

Structurally, there appear to be no obvious differences between females of these species. The sublateral tubercles of the clypeal margin tend to be less distinctly separate from one another in *C. quadridentata,* and the punctures of terga 3 and 4 are less dense and a little finer. But, each species is sufficiently variable that no consistent pattern is clear.

Although males are also clearly similar, the differences in the shape of the protarsal segments, especially the third, will easily separate *C. quadridentata* from *C. exilis.* The presence of conspicuous, short, flattened, plumose, pale hairs on the discs of the fifth and sixth terga is also characteristic of *C. quadridentata* males.

It is possible that the males here associated with *C. quadridentata* do not belong to this species, and that the following species, *C. reflexa,* is the opposite sex of *C. quadridentata.* However, the males here assumed to belong to *C. quadridentata* are much more similar to those of *C. exilis* than are those of *C. reflexa.* They are especially similar in characteristics of the procoxa, the protarsi, and the shape of the apical metasomal tergum. For these reasons, I have assumed these to be the males of *C. quadridentata.*

In addition to the type, I have seen the following material of *C. quadridentata,* all from MEXICO. *GUERRERO:* 1 ♀, 1 ♂, 5 mi S, 2.5 mi E Chilpancingo, 3800 ft elev., 5 Aug. 1962 (University of Kansas Mexican Expedition; UKAN); 1 ♂, 2 mi E Tixtla, 4925 ft elev., 8 Aug. 1962 (Ordway and Naumann; UKAN). *JALISCO:* 2 ♀♀, 1 ♂, 10 mi N

Guadalajara, 16 Oct. 1968 (G.E. Bohart; BBSL); 3 ♀♀, Lake Chapala, 21 Apr. 1957 (A.P. Yerington; LACM); 4 ♀♀, Puerto Vallarta, 25 Jan. 1984 (G.E. Bohart; BBSL); 1 ♀, El Tuito, 25 Sept. 1985 (Parker and Griswold; BBSL); 2 ♀♀, 54 km SE Puerto Vallarta, 29 Sept. 1985 (C.D. Michener; UKAN); 1 ♀, Tamatlan, 1 Oct. 1985 (T. Griswold; BBSL); 2 ♀♀, Chamela, 26–30 Sept. 1985 (F.D. Parker and T.L. Griswold; BBSL); 1 ♀, Río Chamela, 15–24 Apr. 1986 (F.D. Parker; BBSL). *MORELOS:* 1 ♂, Ignacio Bastida, 12 Sept. 1980 (Michener, R. Murillo, J.M. Labougle; UKAN). *OAXACA:* 1 ♀, 23 mi S Matias Romero, 200 ft elev., 25 June 1961 (University of Kansas Mexican Expedition; UKAN); 1 ♀, 10 mi SE Oaxaca, 5300 ft elev., 6 July 1953 (University of Kansas Mexican Expedition; UKAN); 5 ♀♀, 5 ♂♂, 5 mi NW Totolapan, 3800 ft elev., 6 July 1953 (University of Kansas Mexican Expedition; UKAN); 1 ♂, 3 mi SE Yanhuitlan, 17 Sept. 1974 (G.E. and R.M. Bohart; BBSL); 2 ♂♂, 2 mi Cuyeyepeji 3, Mar. 1972 (F. Parker and D. Miller; BBSL); 8 ♀♀, 17 km W Tehuantepec, 8 Sept. 1965 (D.H. Janzen; UKAN), on *Caesalpinia sclerocarpa;* 1 ♀, 35 mi W Tehuantepec, 15 Sept. 1974 (G. Bohart and W. Hansen; BBSL). *PUEBLA:* 20 ♀♀, 7 ♂♂, 3 mi NW Petlalcingo, 4 Mar. 1972 (F. Parker and D. Miller; BBSL); 5 ♂♂, same locality, 6 Aug. 1969 (University of Kansas Mexican Expedition; UKAN); 1 ♂, 9 mi W Izucar de Matamoros, 3 Sept. 1974 (W. Hanson and G. Bohart; BBSL); 1 ♀, 3 mi S Zapotitlan, 2 Mar. 1972 (F. Parker and D. Miller; BBSL). *SAN LUIS POTOSI:* 1 ♀, 3.4 mi NE El Naranjo, 800 ft elev., 5 Sept. 1962 (University of Kansas Mexican Expedition; UKAN). *SINALOA:* 1 ♀, 5 mi E Concordia, 12 Sept. 1970 (G.E. and R.M. Bohart; BBSL). *VERA CRUZ:* 1 ♀, 3 mi SW Paso del Toro, 50 ft elev., 23 June 1961 (University of Kansas Mexican Expedition; UKAN); 1 ♂, Potrero Viejo, 1700 ft elev., 6 June 1949 (W.W. Dalquist; UKAN). *ZACATECAS:* 1 ♀, 10 mi S Jalpa, 17 Sept. 1970 (G.E. and R.M. Bohart; BBSL).

## *Chalicodoma* (*Chelostomoides*) *reflexa*, new species

Figures 8, 18, 29, 39–41

### DIAGNOSIS

Male mandible with prominent process on lower margin; procoxal process prominent; protarsal segments expanded and excavated and probasitarsus with basal row of distally hooked setae on anterior margin; discs of fourth and fifth terga black pubescent. Female unknown.

### DESCRIPTION

**MALE.** Measurements (mm): Holotype HW 2.41; HL 2.67; WL 7.0; TL 9.0. Paratypes: HW 3.18–3.74; HL 2.46–2.97; WL 6.0–7.0; TL 9.0–10.0.

Head about 1.3 times as broad as long; inner eye margins weakly convergent below, upper interorbital distance about 1.1 times lower interorbital distance; in frontal view, preoccipital margin strongly elevated above eyes and ocelli. Mandible (Fig. 19) with large, triangular submedian process on lower margin; apex tridentate, inner tooth large, acute. Labrum normal, apex truncate and margins parallel. Clypeus nearly flat, apical margin weakly incurvate, with a pair of strong submedian tubercles, margin between them weakly convex; coarsely, subcontiguously punctate near base, becoming finely rugosopunctate distad; a weakly defined median impunctate line on basal one-half or less; interspaces slightly to moderately shiny. Supraclypeal area and frons dull, with contiguous moderate punctures (about 0.04 mm diameter); vertex and preoccipital area slightly shiny between fine, subcontiguous punctures; gena shinier, punctures fine to moderate, subcontiguous. Pedicel about 1.5 times longer than first flagellar segment, latter broader than long; second flagellar segment 2.2–2.5 times longer than first. Interocellar distance greater than ocellocular distance; ocellocular distance greater than ocelloccipital distance.

Mesoscutum slightly shiny between moderate, subcontiguous punctures; scutellum similar but a little shinier; metanotum dull, with sparse minute, obscure punctures; mesepisternum mostly dull, moderately and contiguously punctate (rugosopunctate in some areas), but punctures a little more separated below; metepisternum and side of propodeum dull, punctures fine to moderate, contiguous, but variably rugosopunctate in some areas; propodeal disc moderately shiny and sharply tessellate, but with variable fine rugae on either side at base.

Procoxa with sparse ferruginous bristles over entire ventral surface and with dense patch at base of distal process, the process flattened and a little longer than broad. Protarsus broad, concave inner faces of first three segments smooth and shiny; first segment, along anterior margin, with about eight widely spaced, long, ferruginous bristles, which are abruptly curved mesad near their apices; probasitarsus with mastigion; last protarsal segment slender, slightly longer than proximal segment.

First metasomal tergum moderately shiny between fine, subcontiguous punctures; terga 2–4 shiny between fine to moderate punctures, interspaces mostly about one puncture diameter or a little more; tergum 5 similar but punctures mostly subcontiguous; tergum 6 dull, contiguously finely punctate, carina conspicuous in dorsal view, bilobed (Fig. 10), apical margin with prominent lateral teeth, submedian teeth prominent, acute (hidden in dense hairs); exposed sterna slightly to moderately shiny between fine, contiguous to subcontiguous punctures.

Hidden sterna. Fourth sternum hidden but not modified. Sternum 5 (Fig. 39) with lateral portion (="presternite" of Mitchell, 1935) long and narrow; asetose in center (="medasternite" of Mitchell, 1935), with submedian patch of stout, apically curved setae, which become longer laterad and complexely branched; with a pair of long, slender preapical lobes, from tips of which arise a cluster of very long, simple setae curved mesobasad; apical margin with setose median tubercle and sublateral cluster of short, stout, profusely branched setae. Sternum 6 (Fig. 40) with lateral portions about as broad as long; median area with mediobasal cluster of short, simple setae and with lateral complex lobules, closely pectinate distad, bearing a few short, stout, barbed setae and numerous long, simple, acute setae; apical margin straight, simple. Sternum 8 (Fig. 41) with scattered, barbed setae on margin distad of lateral process; preapically constricted and with large distal patch of long, branched setae.

Genitalia (Fig. 29): gonocoxite long and narrow beyond base, apex obliquely capitate; volsella short and broad, apex emarginate; aedeagus slender, slightly constricted below apex, apex truncate, rounded at side.

## TYPE MATERIAL

Holotype male: Estacion Biologia de Chamela, near San Patricio, *JALISCO,* MEXICO, 12 MAY 1980 (S.H. Bullock, #377), in Natural History Museum of Los Angeles County. Paratypes, all MEXICO: *GUERRERO:* 6 ♂♂, 5 mi S, 2.5 mi E Chilpancingo, 3800 ft elev., 5 Aug. 1962 (University of Kansas Mexican Expedition; UKAN); 4 ♂♂, 16 mi N Chilpancingo, 7 Aug. 1962 (N. Marston; UKAN); 2 ♂♂, 17 mi N Chilpancingo, 2550 ft elev., 13 Aug. 1962 (University of Kansas Mexican Expedition; UKAN); 1 ♂, 2 mi E Tixtla, 4925 ft elev., 8 Aug. 1962 (Ordway and Naumann; UKAN). *JALISCO:* 1 ♂, same data as holotype (LACM); 1 ♂, Chamela, 1–8 Oct. 1985 (F.D. Parker and T.L. Griswold; BBSL); 3 ♂♂, Río Chamela, 15–24 Apr. 1986 (F.D. Parker; BBSL); 2 ♂♂, 10 mi N Guadalajara, 16 Oct. 1968 (G.E. Bohart; BBSL); 1 ♂, Chapala, 15 Oct. 1968 (G.E. Bohart; BBSL); 3 ♂♂, Puerto Vallarta, 25 Jan. 1984 (G.E. Bohart; BBSL). *MORELOS:* 5 ♂♂, 4.3 mi W Yautepec, 4000 ft elev., 17 Aug. 1962 (Ordway and Marston; UKAN); 4 ♂♂, 7.3 mi S Yautepec, 3000 ft elev., 16 Aug. 1962 (Ordway and Naumann; UKAN); 3 ♂♂, Ignacio Bastida, 12 Sept. 1980 (Michener, R. Murillo, J.M. Labougle; UKAN). *NAYARIT:* 1 ♂, Ahuacatlan, 18–22 July 1951 (H.E. Evans; UKAN); 5 ♂♂, 9 mi NW Santa Isabella, 10 Mar. 1972 (F. Parker and D. Miller; BBSL). *OAXACA:* 7 ♂♂, 17 km W Tehuantepec, 8 Sept. 1965 (D.H. Janzen; UKAN), on *Caesalpinia sclerosa;* 1 ♂, 11 mi N Miltipec, 3 Mar. 1972 (F. Parker and D. Miller; BBSL); 2 ♂♂, 5 mi NW Totolopan, 3800 ft elev., 6 July 1953 (University of Kansas Mexican Expedition; UKAN), on *Lonchocarpus;* 1 ♂, 17 mi E Totolopan, 16 Sept. 1974 (W. Hanson, G. Bohart; BBSL). *PUEBLA:* 3 ♂♂, 3 mi NW Petlalcingo, 4 Mar. 1972 (F. Parker and D. Miller; BBSL). *SINALOA:* 1 ♂, 31 km N Mazatlan, 75 m elev., 29 Sept. 1976 (C.D. George and R.R. Snelling; LACM), on *Antigonon leptopus;* 2 ♂♂, Escuintla, 25 June 1956 (LACM); 2 ♂♂, 9 mi NE Chupaderos, 2 Mar. 1972 (F. Parker and D. Miller; BBSL); 1 ♂, Guamachil, 27 Oct. 1965 (G.E. and A.S. Bohart; BBSL). *SONORA:* 3 ♂♂, Alamos, 7 Sept. 1970 (G.E. and R.M. Bohart; BBSL); 1 ♂, Río Cuchuhaqui, 7 mi S Alamos, 25 July–7 Aug. 1953 (F.S. Truxal; LACM); 1 ♂, Río Cuchuhaqui, 8 mi S Alamos, 1–13 Apr. 1975 (A. Brewster; LACM), on *Cercidium;* 1 ♂, same, except on *Prosopis.*

## ETYMOLOGY

The specific epithet is a Latin word for bent and refers to the row of distally reflexed setae on the probasitarsus.

## DISCUSSION

Although the male *C. reflexa* resembles males of most other species with modified protarsi, this species is easily separated from all except *C. otomita* by possessing a row of hooked setae basad on the anterior, inner margin of the probasitarsus. Males of *C. reflexa* may be separated from those of *C. otomita* by the presence of dark, simple hairs on the discs of the last three terga, rather than appressed, more or less fulvous, plumose hairs. Also, in *C. reflexa,* the fourth protarsal segment is asymmetrical, with the anterior lobe strongly produced; in *C. otomita* the fourth protarsal segment is symmetrical.

The unknown female of *C. reflexa* is probably similar to that of *C. otomita* but will likely have whitish rather than fulvous pubescence. Probably, too, the discs of terga 4 and 5 will be dark pubescent.

Known floral records include only two families. BIGNONIACEAE: *Antigonon leptopus.* FABACEAE: *Caesalpinia sclerocarpa, Cercidium* sp., *Lonchocarpus* sp., *Prosopis* sp.

### *Chalicodoma* (*Chelostomoides*) *subexilis* (Cockerell)

*Megachile subexilis* Cockerell, 1903:292; ♀.
*Megachile semiexilis* Cockerell, 1908:292; ♀♂.
*Megachile* (*Chelostomoides*) *subexilis:* Mitchell, 1937:384, 385, 394–396; ♀♂. Mitchell, 1956:131, 134, 137; ♀♂.

Among those species in which the female possesses a preapical groove on tergum 6, the female of *C. subexilis* is easily recognized by the exceptionally prominent submedian tubercles of the clypeal margin and the presence of a pubescent fascia on the apical margin of tergum 5. The male differs from others with a ventral mandibular process and grooved protarsi in possessing only reclinate, simple setae over most of the procoxa (which has a prominent distal process) and in lacking a mastigion at the base of the probasitarsus.

This is a moderately common montane species that ranges from Nebraska and Colorado west to California.

Nectar and/or pollen sources encompass 27 plant genera in 11 families. Known floral associations include the following. AMARYLLADACEAE: *Allium* sp. ANACARDACEAE: *Rhus trilobata.* ASTERACEAE: *Erigeron neomexicanus, Helenium* sp., *Helianthus* sp., *Verbesina encelioides.* CACTACEAE: *Opuntia* sp. CAPPARIDACEAE: *Cleome serrulata.* FABACEAE: *Amorpha* sp., *Cracca edwardsii, Desmodium batocaulon, Lathyrus arizonica, L. graminifolius, L. odoratus, Lotus* sp., *L. corniculatus, L. oroboides, Lupinus palmeri, Medicago sativa, Melilotus* sp., *Oxytropis lambertii, Phaseolus* sp., *Psoralea tenuiflora, P. wrightii, Trifolium* sp., *T. pinetorum, T. pratense, Vicia* sp., *V. pulchella, V. villosa.* GERANIACEAE: *Geranium* sp. HYDROPHYLLACEAE: *Phacelia* sp. LAMIACEAE: *Marrubium vulgare, Monarda* sp., *M. austromontana, M. pectinata, Salvia* sp. RHAMNACEAE: *Ceanothus fendleri.* ROSACEAE: *Chamaebatiaria millefolium.*

Nests have been found in adobe walls, sandstone, and in borings in wood. Known megachilid cleptoparasites include *Dioxys pomonae* Cockerell (Hurd, 1958) and *Coelioxys gilensis* Cockerell (Hicks, 1927).

## Group II (*georgica* Group)

**GROUP CHARACTER.** Male mandible slender, tridentate, without ventral process, hypostomal acetabulum present; male protarsal segments broad, flat, basitarsus densely setose on inner surface; female clypeal disc simple, apical margin strongly tuberculate, but without median tubercle; female tergum 6 without preapical groove.

**INCLUDED SPECIES.** *Chalicodoma georgica* (Cresson).

The one species in this group flies primarily during the summer and fall months and is limited to the southeastern United States. Although most floral records are from legumes, *C. georgica* appears to be polylectic.

Because of the simple clypeal structure, females most closely resemble those of Group I (*exilis* group) but are easily separated by the lack of a preapical groove on tergum 6. Males, by virtue of the broad, flattened protarsus, resemble those of Group III (*occidentalis* group) but have the probasitarsus setose rather than densely tomentose on the inner surface. Additionally, males of *C. georgica* have a prominent procoxal process that is about twice longer than its basal breadth.

### *Chalicodoma* (*Chelostomoides*) *georgica* (Cresson)

*Megachile georgica* Cresson, 1878:123; ♀♂.
*Megachile penicillata* Cockerell, 1915:536; ♀.
*Megachile* (*Chelostomoides*) *georgica:* Mitchell, 1937:384, 386, 396–398; ♀♂. Mitchell, 1956:135, 137; ♀♂.

Among those species in which the female lacks a transverse groove on tergum 6 and which possess a stout, quadridentate mandible, the female may be recognized by the transverse apical clypeal margin with only weak and irregular denticulae. The clypeal disc is flat and sparsely covered with simple setae; only at the sides are there conspicuous, plumose hairs. The male falls within that small group that is characterized by possessing broad, flat, protarsal segments. From the only other species with similar tarsi (*C. davidsoni, C. occidentalis,* and *C. prosopidis*), males of *C. georgica* may be separated by the prominent procoxal process and the presence of reclinate, simple setae on the inner surface of the probasitarsus.

This is an eastern species, ranging from Maryland and New Jersey south to Florida; westward, the range extends to Arkansas and eastern Texas. A polylectic species, *C. georgica* has been taken on plants belonging to 21 genera, representing eight families; the bulk of the records are from legumes. Known floral associations for *C. georgica* include the following. ASTERACEAE: *Chrysopsis* sp., *Erigeron* sp., *Helenium* sp., *Helianthus* sp. CLETHRACEAE: *Clethra alnifolia.* ERICACEAE: *Vaccinium* sp. FABACEAE: *Afzelia cassinoides, Amorpha* sp., *Baptisia tinctoria, Calactia* sp., *Crotalaria* sp., *Desmodium* sp., *Melilotus* sp., *Phaseolus* sp., *Psoralea* sp., *Tephrosia virginiana.* HYPERICACEAE: *Hypericum* sp. LAMIACEAE: *Pycnanthemum hypsifolia, Stachys* sp. LOBELIACEAE: *Lobelia* sp. SCROPHULARIACEAE: *Penstemon* sp.

Krombein (1967) reared the parasitoides *Leucospis affinis floridana* Cresson (Leucospidae) and *Coelioxys modesta* F. Smith (Megachilidae) from nests of *C. georgica* in Florida. The flight period extends from March to November (Mitchell, 1962).

## Group III (*occidentalis* Group)

**GROUP CHARACTERS.** Male mandible tridentate and moderately long, with prominent ventral process; hypostomal acetabulum present, exposed; male protarsal segments broad, flattened, and basal segments densely tomentose on inner surface; female mandible long, with three or four apical teeth and with upper, outer carina more or less elevated near base; female clypeal disc bizarre and apical margin concealed and simple; female tergum 6 without preapical groove.

**INCLUDED SPECIES.** *Chalicodoma davidsoni* (Cockerell), *C. occidentalis* (W. Fox), and *C. prosopidis* (Cockerell).

The three species of this group are found in arid and semiarid regions of the southwestern United States and adjacent Mexico. Two species occur in lowland habitats, and one is known only from the mountains of southern and central California. The two lowland species are polylectic and the montane species appears to be oligolectic.

### *Chalicodoma* (*Chelostomoides*) *davidsoni* (Cockerell)

Figures 4, 61, 62

*Megachile davidsoni* Cockerell, 1902:70; ♀.
*Megachile occidentalis* var. *leucotricha* Cockerell, 1902:137; ♂.
*Megachile* (*Chelostomoides*) *davidsoni:* Mitchell, 1937:384, 401–402; ♀♂. Mitchell, 1956:132, 134, 137; ♀♂.

Both sexes of this species, the largest in the subgenus, are easily recognized by the characters cited in the key. The large, prominent processes on the mandible and clypeus are characteristic for the female as are the subcarinate clypeus and expanded, flattened protarsi of the male, but with the prodistitarsus much longer than the other segments.

Although Hurd (1979) cited *C. davidsoni* from Arizona, I have seen specimens only from California, where all previous records are from the San Gabriel, San Bernardino, and San Jacinto mountain ranges. However, a series of specimens extends the range north along the western slopes of the Sierra Nevada to Fresno Co.: 2 ♀♀, 18 ♂♂, 5.5 mi NE Tollhouse, 26 June 1982 (J.A. Halstead; HALS), on *Dicentra* sp. probably *chrysantha;* 1 ♀, Clingan's Junction, Hwy. 180, 3500 ft elev., 7 July 1955 (R.Y. Berg; UCB), on *D. chrysantha.*

Available records show a flight period extending from late May to mid-July in southern California.

Although the females are presumed oligoleges on *Dicentra* for pollen, *C. davidsoni* has been recorded from the following plants. ASTERACEAE: *Senecio* sp. FABACEAE: *Lathyrus* sp., *Lupinus austromontanus.* FUMARIACEAE: *Dicentra* sp., *D. chrysantha.* SCROPHULARIACEAE: *Penstemon grinnellii.* STERCULIACEAE: *Fremontia* sp.

### *Chalicodoma* (*Chelostomoides*) *occidentalis* (W. Fox)

Figures 69, 70

*Megachile occidentalis* W. Fox, 1894:117; ♂.
*Megachile prosopidis* var. *testudinis* Cockerell, 1924:550; ♀.
*Megachile* (*Chelostomoides*) *ignacensis* Mitchell, 1934:352; ♀. NEW SYNONYMY.
*Megachile* (*Chelostomoides*) *occidentalis:* Mitchell, 1937:384, 385, 398–401; ♀♂ (in part). Mitchell, 1956:132, 134, 137; ♀♂ (in part).

The name *C. occidentalis* is not used here in the sense of Mitchell (1934) and subsequent authors. It is my belief that *C. occidentalis* has been persistently misidentified and that the correct name for the species long known as *C. occidentalis* is *C. prosopidis.*

Fox (1894) described *Megachile occidentalis* from a single male from San Ignacio, Baja California Sur, Mexico. When Mitchell (1934) revised the species of *Chelostomoides,* he associated this specimen with other males ranging from southern California to western Texas, and with females that had been described by Cockerell (1900) as *M. prosopidis* from Mesilla, New Mexico. Although I cannot prove that this association is incorrect, I believe, nevertheless, that this is the case. The type locality of *C. occidentalis* is in Baja California Sur. And, although I have seen a number of males from this part of Mexico that match very well with the type, I have seen no females from there that correspond to the interpretation of Mitchell (i.e., *C. prosopidis*). These males are consistently associated with those females described by Mitchell (1934) as *M. ignacensis.* It should be noted that the type of *M. ignacensis* was collected at the same time and place as the type of *M. occidentalis.*

The two species, as represented by the female types (*M. prosopidis* and *M. ignacensis*), are so very similar in mandibular and clypeal structure that their close relationship appears to be inarguable. However, the mandible of the *C. occidentalis* female has a prominent, blunt, tooth-like process on the upper margin (Fig. 70), whereas in *C. prosopodis* the dorsal ridge is low and convex (Fig. 72). The lateral processes of the clypeus are broad, and the apex of the median process is transverse or weakly convex in *C. occidentalis* (Fig. 69). In *C. prosopidis* the lateral processes are corniform, and the median process is distinctly produced in the middle (Fig. 71). Finally, in females of *C. occidentalis,* the distance from the base of the clypeus to the apex of the median lobe is much less than the interantennal distance, whereas in *C. prosopidis* it is subequal to the interantennal distance.

In view of the obvious similarities of the females of *C. occidentalis* and *C. prosopidis,* the males should also be similar to one another. In fact, at this point, I am unable to distinguish two species on the basis of the males. For the present, males can only be separated geographically.

There is no demonstrable evidence that females of the *C. prosopidis* type are present in central and southern Lower California. Instead, in this portion of Mexico, they are replaced by the females that I presume are truly those of *C. occidentalis. Chalicodoma occidentalis,* as interpreted here, is limited to the Lower California peninsula; records of *C. occidentalis* from the United States and mainland Mexico should be transferred to *C. prosopidis.*

The few specimens recorded here will augment the limited information on this species. MEXICO, *BAJA CALIFORNIA:* 2 ♀♀, 6 mi S Okie Landing, 13 June 1968 (M. Cazier et al.; ARSU); 1 ♂, Cataviña, 19 June 1983 (L. Stange and R. Miller; FSCA); 1 ♀, Cerro de Cedros, Isla Cedros, 1 July 1983 (D.K. Faulkner; SDM); 2 ♀♀, 13 km NW Rosarito, 9 Sept. 1977 (R.R. Snelling; LACM); 1 ♂, same except (E.M. Fisher and R.L. Westcott; CAS); 1 ♀, San Antonio Microwave Tower, 27 Aug. 1982 (Faulkner and Brown; SDM). *BAJA CALIFORNIA SUR:* 1 ♀, 13 mi SW La Purissima, 2 July 1968 (M. Cazier et al.; ARSU); 1 ♀, 32 mi NW La Paz, 15 Mar. 1980 (J.L. Neff; NEFF), on *Cercidium peninsulare;* 1 ♀, 1 ♂, 52 mi NW La Paz, 15 Mar. 1980 (J.L. Neff; NEFF), on *C. peninsulare;* 1 ♂, 10 mi S La Paz, 16 Oct. 1972 (C.D. Michener; UKAN); 1 ♂, 20 km NW La Paz, 5 Oct. 1975 (R.R. Snelling; LACM); 1 ♀, 3 mi S La Paz, 13 Mar. 1980 (J.L. Neff; NEFF), on *C. peninsulare;* 1 ♂, 2.5 mi S jct. Hwys. 1 and 19, 27 Aug. 1982 (Faulkner and Brown; SDM); 1 ♂, 4 km N Los Barriles, 10 m elev., 4 Sept. 1977 (R.R. Snelling; LACM); 1 ♀, 19 mi SE El Cien, 27 Sept. 1981 (D. Faulkner and F. Andrews; SDM); 1 ♂, Mulegé, 24 Sept. 1981 (D. Faulkner and F. Andrews; SDM); 1 ♀, 12.8 mi SE Santa Rosalia, 21 Sept. 1981 (D. Faulkner and F. Andrews; SDM); 21 ♀♀, 1 ♂, 5 mi NW San Ignacio, 13 and 19 Sept. 1983 (R.R. Snelling; LACM), on *Tephrosia tenella.*

The presently known floral records are all within the family Fabaceae.

### *Chalicodoma* (*Chelostomoides*) *prosopidis* (Cockerell)

Figures 71, 72

*Megachile prosopidis* Cockerell, 1900:16; ♀.
*Megachile* (*Chelostomoides*) *occidentalis:* Mitchell, 1937:384, 385, 398–401; ♀ (in part). Mitchell, 1956:132, 134, 137; ♀ (in part).

This is a moderately common and widely distributed species in arid western North America, from Texas to California. It was long known as *C. occidentalis,* but that name must now be applied to a morphologically similar species limited to the Lower California peninsula of Mexico. For separation from *C. occidentalis,* see discussion under that species.

Previous records of this bee in California have been limited to the southern counties (Imperial, Inyo, Los Angeles, Riverside, San Bernardino, and San Diego Counties). Mitchell (1937) cited a specimen from Los Mochis, Sinaloa, Mexico.

The following records extend the known range in California and Mexico. UNITED STATES, *CALIFORNIA,* Fresno Co.: 1 ♂, Fresno, 22 July 1970 (E.A. Kane; CDFA), on *Helianthus;* 2 ♀♀, Fresno, 27 and 31 May 1982 (J. Halstead; HALS); 1 ♂, 8 mi W Kerman, 2 Aug. 1960 (R.R. Snelling; LACM), on *Wislizenia refracta;* 1 ♂, 4 mi SE Orange Cove, 18 June 1957 (R.R. Snelling; LACM). Madera Co.: 1 ♂, Madera, 15 June 1982 (J. Halstead; HALS); 1 ♂, 8 mi S Madera, 17 June 1957 (R.R. Snelling; LACM), on *Helianthus.* Stanislaus Co.: 2 ♂♂, Turlock, 2 May and 15 June 1953 (R.R. Snelling; LACM); 1 ♀, Turlock, 4 Oct. 1954 (R.R. Snelling; LACM), on *Citrullus vulgaris.* MEXICO, *CHIHUAHUA:* 1 ♂, 10 mi N Chihuahua, 22 Sept. 1950 (R.M. Bohart; UCD); 1 ♂, Santo Niño, 10 Aug. 1968 (T.A. Sears, R.C. Gardner, C.S. Glaser; UCD); 1 ♂, 2 mi N Temoris, 17 Aug. 1968 (same; UCD); 8 ♂♂, 4 mi NW Choix, 27 Aug. 1968 (same; UCD). *SONORA:* 2 ♂♂, La Aduana, 12 June 1961 (A.S. Menke and L.A. Stange; LACM); 2 ♀♀, 5 mi E Navojoa, 2 Aug. 1960 (Arnaud, Ross, Rentz; CAS); 1 ♂, Río Chuchuhaqui, 7 mi S Alamos, 25 July–7 Aug. 1953 (F.S. Truxal; LACM); 5 ♂♂, 6 km NNW San Carlos, 11–15 July 1983 (E.M. Fisher; CDFA). *ZACATECAS:* 1 ♂, 22°40'N, 104°03'W, 7 Sept. 1984 (W.J. Pulawski; CAS).

*Chalicodoma prosopidis* is primarily a summer flying species with the bulk of the flight records during the months of June, July, and August. Floral records include plants of 30 genera, representing 14 families. AGAVACEAE: *Nolina parryi.* ANACARDIACEAE: *Schinus molle.* ASTERACEAE: *Chrysothamnus* sp., *Geraea canescens, Helianthus* sp., *Lepidospartum squamatum, Pectis papposa, Pluchea camphoratum, Senecio* sp., *Vernonia* sp. BIGNONIACEAE: *Chilopsis linearis.* BRASSICACEAE: *Stanleya pinnata.* CAPPARIDACEAE: *Cleome* sp., *Wislizenia refracta.* CUCURBITACEAE: *Citrullus vulgaris.* EUPHORBIACEAE: *Croton californicus.* FABACEAE: *Cercidium floridum, Hoffmannseggia* sp., *H. densiflora, Lotus* sp., *Medicago sativa, Parkinsonia* sp., *P. aculeata, Prosopis* sp., *Psorothamnus emoryi, P. scoparius, Vicia cracca.* HYDROPHYLLACEAE: *Phacelia* sp. LAMIACEAE: *Marrubium vulgare.* TAMARICACEAE: *Tamarix gallica.* VERBENACEAE: *Duranta plumieri, Lippia nodiflora.* ZYGOPHYLLACEAE: *Larrea tridentata.*

The meloid beetle *Nemognatha lurida* LeConte has been reared from nests of this bee (Hurd, 1979). Nests have been found in a variety of situations, including adobe and brick walls, dead wood, and trap nests.

## Group IV (*abacula* Group)

**GROUP CHARACTERS.** Male mandible short, broad, and obscurely quadridentate, without ventral process; hypostomal acetabulum absent; male protarsal segments slender, inner surface flat and densely setose; female mandible short and broad, with four apical teeth; female clypeal disc unmodified and apical margin produced in middle and denticulate or tuberculate, with median denticle; male clypeal margin with prominent medial tubercle; female tergum 6 without preapical groove.

**INCLUDED SPECIES.** *Chalicodoma abacula* (Cresson) and *C. alucaba,* n. sp.

The two species in this group range from central Mexico south to Costa Rica. Both appear to be uncommon, and little is known about their floral biology.

### *Chalicodoma* (*Chelostomoides*) *abacula* (Cresson)

Figures 14, 15

*Megachile abacula* Cresson, 1878:130–131; ♀.
*Megachile gualanensis* Cockerell, 1912:27; ♀. NEW SYNONYMY.

The types of *M. abacula* and *M. gualanensis,* both females, are in the USNM, and I have examined them and find no differences sufficient to warrant their separation.

Specimens of C. *abacula* from Mexico and Guatemala are easily recognized by the presence of numerous reclinate, plumose hairs on the discs of terga 4 and 5 of both sexes; most commonly, these hairs are fulvous. Males are further characterized by the short mandibles without a ventral process, the prominent median tubercle on the clypeal margin, the simple procoxa and protarsus, and the evanescent carina of tergum 6. The females also possess short, broad mandibles and the clypeus is subangularly convex from side to side, with the apical margin a little protuberant in the middle and with a prominent median tubercle. The mesepisternum is rugosopunctate. Both sexes also possess conspicuous, blackish hairs among the white clypeal hairs. Specimens from Costa Rica differ from those I have seen from Mexico and Guatemala. The pubescence of the abdominal terga is almost invariably whitish rather than fulvous and, in both sexes, the reclinate, plumose discal hairs are greatly reduced in number. Usually none are present on the disc of tergum 4 in both sexes. Tergum 5 usually has numerous such hairs in the male, but in the female they are sparse and generally limited to the posterior one-half, or less, of the segment.

These Costa Rican specimens are very similar to *C. alucaba,* described below, and, in the absence of associated males, it may prove difficult to distinguish between the two species. At present, *C. alucaba* is known only from Mexico, where the characteristics of *C. abacula* are best defined. It seems reasonable to assume that character displacement is involved where the two species are sympatric. Much more material of both species, from additional localities, will be necessary before it is possible to understand their relationship.

The following are new records for *C. abacula.* MEXICO, *CHIAPAS:* 1 ♀, Francia, 8 mi NE Cintalapa, 3 Apr. 1953 (R.C. Bechtel and E. I. Schlinger; BBSL). *OAXACA:* 4♀♀, 1 ♂, 4 mi N Pochutla, 150 m elev., 11 Oct. 1975 (J.L. Neff, NEFF), on *Salvia.* HONDURAS: 1 ♂, Finca San Francisco, 30 Jan. (W.P. Cockerell; BBSL); 1 ♂, locality unreadable, Feb. (M.A. Willows; BBSL). NICARAGUA: 1 ♀, San Marcos (Baker; LACM). COSTA RICA, *GUANACASTE:* 3 ♂♂, La Pacifica, 4 mi NW Cañas, 25–30 Jan. 1972 (P.A. Opler; UCB), on *Melanthera nivea;* 1 ♀, 1 ♂, same locality and collector, 1972 on *M. nivea;* 2 ♀♀, same locality and collector, 15–20 Sept. 1973, on *Cordia collococca;* 158 ♀♀, 6 ♂♂, Liberia, 15–16 Feb. 1972 (P.A. Opler; UCB), on *Andira inermis;* 36 ♀♀, 4 ♂♂, same locality and collector, 23–26 Feb. 1972, on *A. inermis;* 6 ♀♀, same locality and collector, 1 Mar. 1972, on *A. inermis;* 1 ♀, Comelco, 8 km NW Bagaces, 25 Mar. 1972, on *Lonchocarpus costaricensis* (all UCB).

The above floral records represent the following families. ASTERACEAE: *Melanthera nivea.* BORAGINACEAE: *Cordia collococca.* FABACEAE: *Andira inermis, Lonchocarpus costaricensis.*

## *Chalicodoma* (*Chelostomoides*) *alucaba,* new species

Figures 1, 4, 20, 30, 36–38

### DIAGNOSIS

Male with unmodified protarsus and without ventral mandibular process; carina of tergum 6 low and inconspicuous, weakly bilobate; clypeus with prominent median process, but lateral processes weak; third mandibular tooth with a small, conical tubercle on inner surface. Female with short, broad mandible and tergum 6 without preapical groove; apical margin of clypeus produced and with small median process and some erect fuscous to blackish hairs on disc; tergum 5 without traces of marginal hair band.

### DESCRIPTION

**FEMALE.** Measurements (mm): HW 2.71–2.95; HL 2.24–2.43; WL 5.3–5.6; TL 9.4–10.5.

Head about 1.2 times as broad as long; inner eye margins very weakly convergent below, upper interorbital distance less than 1.1 times lower interorbital distance; in frontal view, vertex-preocciput elevated above ocelli by considerably less than transverse diameter of anterior ocellus. Mandible robust, apical margin with four well-defined teeth and with a weak tooth between third and fourth (inner) teeth. Sides of labrum mostly subparallel, narrowed preapically, without median, preapical seta-pit. Apical margin of clypeus slightly produced and with low median denticle, margin on either side irregular but without definite denticles; disc with very narrow median impunctate line, broadest basad, otherwise contiguously, moderately punctate, median line and interspaces smooth and shiny. Supraclypeal area shiny between contiguous, moderate punctures, but interspaces progressively less shiny above, merging to slightly shiny interspaces between contiguous, moderate punctures of frons; vertex and preocciput similar to frons, but with some irregular interspaces up to one-half puncture diameter. Gena, at widest, about one-half as wide as eye, shiny between contiguous, fine to moderate punctures. Pedicel about twice longer than first flagellar segment and less than twice longer than second; first flagellar segment broader than long; median flagellar segments slightly longer than broad. Interocellar distance greater than ocellocular distance, each distinctly greater than ocelloccipital distance.

Mesoscutum and scutellum moderately shiny between mostly contiguous, moderate punctures, scutellum with a few coarse punctures; mesepisternum, metepisternum, and side of propodeum similar, with punctation on anterior portion of mesepisternum tending toward rugosopunctate.

Discs of terga 1–5 moderately shiny, that of first tergum with subcontiguous, fine to moderate punctures, those of terga 2–5 similar, but punctures a little more separated and with fewer fine punctures; depressed apical margins with contiguous, fine punctures at base, but with narrow, impunctate rims; tergum 6 slightly shiny between contiguous, fine punctures; preapical groove absent.

Integument generally blackish, flagellum and legs dark reddish brown. Tegula medium brown, becoming transparent yellowish brown toward margins. Wings transparent light brown; veins and stigma dark to medium brown.

Pilosity about as in other *Chelostomoides*, but clypeal disc with a few light brownish hairs, frons and vertex with numerous dark brown to blackish hairs; humeral angle of pronotum with flocculent hair patch; terga 2–5 with basal fasciae of appressed, plumose, white hairs and terga 2–4 with narrow apical fasciae of similar hairs, tergum 5 without apical band; terga 2–5 with sparse, very short, simple, yellowish to brownish hairs across discs and a few long, simple, whitish hairs at sides; tergum 6 with short, subappressed, short-plumose, pale hairs; scopa whitish on sterna 2–5, dark brown on 6.

**MALE.** Measurements (mm): Holotype HW 2.71; HL 2.24; WL 5.2; TL 8.3. Paratypes: HW 2.62–2.90; HL 2.14–2.52; WL 5.1–5.8; TL 7.5–8.7.

Head about 1.2 times as broad as long; eyes weakly convergent below, upper interorbital distance about 1.2 times lower interorbital distance; preoccipital margin arcuately produced above ocelli by about diameter of anterior ocellus. Mandible (Fig. 20) weakly quadridentate, second (subapical) tooth very low and blunt, interspace between third and fourth teeth broad and deep; a low, conical tubercle present on inner side of fourth tooth. Labrum as in female. Apical margin of clypeus nearly straight between weak lateral tubercles and with large median tooth (Fig. 1); disc dull, finely to moderately rugosopunctate. Frons slightly shiny, finely rugosopunctate, grading to contiguously to subcontiguously, moderately punctate on vertex-preocciput. Gena, in profile, nearly as wide as eye, with moderate punctures. Pedicel about twice longer than first flagellar segment, and about as long as second; middle flagellar segments about 1.5 times longer than wide. Interocellar distance less than ocellocular distance, latter about equal to ocelloccipital distance.

Mesosoma about as described for female.

Metasomal terga 1–5 about as in female, but apical margins transparent yellowish and not vertically depressed from discs; carina of tergum 6 low and obscure, with very weak median emargination, apical margin without traces of lateral or submedian teeth.

Hidden sterna and genitalia (Figs. 30, 36–38).

Color as described for female.

Pilosity about as in female, except metasomal terga 1–3 with apical hair bands incomplete and present as lateral patches only, terga 4–5 entirely devoid of apical hair bands; tergum 6 without basal hair band, disc with short, sparse, simple hairs only.

### TYPE MATERIAL (MEXICO)

Holotype male: 9.2 km W Guadalajara, *JALISCO,* 8–9 Sept. 1976 (C.D. George and R.R. Snelling), in LACM. Paratypes: 2 ♂♂, same data as holotype; 1 ♂, 10 mi N Guadalajara, *JALISCO,* 16 Oct. 1968 (G.E. Bohart); 1♂, 30 mi NE Guadalajara, *JALISCO,* 17 Sept. 1970 (R.M. Bohart); 1 ♂, 10 mi S Jalpa, *ZACATECAS,* 17 Sept. 1970 (G.E. and R.M. Bohart); 1 ♀, Juchipila, *ZACATECAS,* 17 Oct. 1968 (G.E. Bohart); 1 ♀, 5 mi N Chila, *PUEBLA,* 14 Oct. 1975 (J.L. Neff); 1 ♀, Concordia, *SINALOA,* 12 Mar. 1972 (F.D. Parker and D.R. Miller). Paratypes in BBSL, LACM, and UCD.

### ETYMOLOGY

The specific name is that of the presumed nearest relative, *C. abacula,* spelled in reverse.

### DISCUSSION

Since the most distinctive features of this species are exhibited by the males, I have departed from my usual procedure in this paper in selecting this sex for the holotype. In addition, the association of the two sexes is only presumptive; the few females may prove to be only variants of *C. abacula.*

The females here associated with *C. alucaba* are very similar to those of *C. abacula.* Females of the latter species commonly have much, or all, of the disc of metasomal tergum 5 covered by short, plumose, appressed hairs. These hairs are usually whitish in Mexican specimens but may be yellowish, as in some from Costa Rica. Similar hairs may also be present, though sparse, on the disc of tergum 4. The apical margin of tergum 5 has a complete band of similar hairs; the band is sometimes interrupted in the middle, apparently due to abrasion. The few females here presumed to be those of *C. alucaba* have no plumose hairs on the discs of terga 4 and 5, and there is no apical pubescent fascia on 5.

Females and males of both species possess conspicuous, very long, brownish to blackish hairs on the frons and similar hairs are also conspicuously present on the clypeus of both sexes of *C. abacula.* Although they are present on the clypeus of *C. alucaba,* they tend to be light yellowish brown in that species and are much less conspicuous.

The male of *C. alucaba* is easily recognized by the presence of a minute denticle on the inner side of the fourth mandibular tooth; this feature appears to be unique within the New World fauna. Additionally, the unusually prominent median denticle of the clypeal margin is characteristic of the *C. alucaba* male.

## Group V (*armaticeps* Group)

**GROUP CHARACTERS.** Male mandible stout and tridentate, with small ventral process; hypostomal acetabulum absent; male first flagellar segment about one-third as long as second; male protarsal segments slender and densely setose on inner surfaces; female mandible stout and obscurely quinquedentate; female clypeal disc bizarre, apical margin exposed and without denticles; supraclypeal process present; female metasomal tergum 6 without preapical groove.

Only the Cuban species *C. armaticeps* is assigned to this group; as unusual combination of character states obscures the relationships of this species. The male has a small triangular process at the midlength of the ventral margin of the mandible (as in Groups I–III) but the protarsal segments are slender and unmodified (as in Groups IV and VI–X). The female face is bizarre, but the mandibles are stout and obscurely five-toothed. Particularly noteworthy of the female is the presence of a large, curved supraclypeal process, a unique feature within known *Chelostomoides.*

## *Chalicodoma* (*Chelostomoides*) *armaticeps* (Cresson)

Figures 75–78

*Megachile armaticeps* Cresson, 1869:296; ♀.

Cresson (1869) described this species from a single female from "Cuba"; the type is in the Gundlach collection at the Academia de Ciencias de Cuba, in Havana (Alayo, 1970). According to Alayo, this species is rare and is known only from the south coast of Oriente Province. I have examined a single pair of specimens collected by P. Alayo at Juragua, Oriente Province, Feb. 1959 (UKAN).

Although female *Chelostomoides* often are characterized by bizarre clypeal and/or mandibular configurations, the female of *C. armaticeps* is the most grotesque of any species known to me. From each side of the clypeus, a large, flattened lobe projects at right angles to the face. Between these lobes, at the apical margin, is an erect T-shaped protuberance. Another process originates on the supraclypeal area; it is erect and thin, but abruptly curved toward the median clypeal process (Figs. 75, 76).

Aside from these facial features the female is rather ordinary. The mandible is short and broad, with five apical teeth. The two middle teeth are fused and difficult to distinguish, and the two innermost teeth (similarly fused) are separated from the middle tooth-pair by a deep, narrow excision. There is no basal mandibular prominence. The sixth metasomal tergum is without a transverse preapical groove.

A flocculent hair patch is present at each side of the pronotum and similar hairs are present along the margins of the mesoscutum adjacent to the tegulae. There are also short notaular patches of short, flocculent hairs. Metasomal terga 1–5 each possess a narrow apical band of appressed, plumose, white hairs; terga 2 and 3 additionally have weak postgradular bands of pale hairs. The scopa is mostly pale but is black on the last segment.

The male of *C. armaticeps* is much less remarkable in appearance. The mandible is stout and tridentate; a triangular process is present at about midlength on the ventral margin, but the process is relatively small (Fig. 77). The apical margin of the clypeus is thin and slightly protuberant, weakly concave in the middle (i.e., weakly bilobate medially); the disc is mostly coarsely and contiguously punctate but medially with a broad impunctate line that extends from the base nearly to the apical margin. A small interantennal tubercle is present at the lower end of the frontal suture.

The male procoxa has an apical spine; this spine is erect and longer than its basal breadth; the disc of the segment is largely bare, with only scattered, short, plumose, pale hairs; longer plumose hairs are present along the margins and across the base. The protarsal segments are simple; i.e., they are slender and the inner surfaces are densely covered by short, stiff, simple hairs. The base of the probasitarsus lacks a mastigion.

The discal carina of metasomal tergum 6 of the male is strongly protuberant and with a deep median emargination (Fig. 78). The lateral teeth on the apical margin of tergum 6 are prominent and angulate; the median teeth are present as long, low, rounded lobes. Genitalia and associated structures were not extracted from the one specimen available to me.

Pilosity of the mesosoma is much the same as that of the female described above. Apical hair bands are present, but incomplete, on metasomal terga 1–5, increasingly more broadly interrupted on succeeding segments. Terga 3–6 possess distinct postgradular pubescent fasciae.

## Group VI (*rugifrons* Group)

**GROUP CHARACTERS.** Male mandible slender, tridentate, without ventral process; hypostomal acetabulum absent; male first flagellar segment one-third, or less, as long as second; male protarsal segments slender, densely setose on inner surface; female mandible slender to very slender, tridentate; female clypeal disc bizarre, apical margin concealed and without denticles; female tergum 6 without preapical groove.

**INCLUDED SPECIES.** *Chalicodoma browni* (Mitchell), *C. chilopsidis* (Cockerell), *C. discorhina* (Cockerell), *C. lobatifrons* (Cockerell), *C. odontostoma* (Cockerell), and *C. rugifrons* (F. Smith).

This is a group found primarily in the arid and semiarid regions of the southwestern United States and adjacent Mexico, but with one species (*C. rugifrons*) found in the eastern United States.

## *Chalicodoma* (*Chelostomoides*) *browni* (Mitchell)

Figures 2, 5, 57, 58

*Megachile* (*Chelostomoides*) *browni* Mitchell, 1934: 354; ♂.

*Megachile* (*Chelostomoides*) *felipiana* Mitchell, 1937:405; ♀.

*Megachile* (*Chelostomoides*) *browni:* Timberlake, 1957:132; ♀♂.

Morphologically, *C. browni* is most similar, in both sexes, to *C. odontostoma*. Females of *C. browni* are easily recognized by the characteristic broad, lateral clypeal lobes (Fig. 50). Males of the two species are much more similar. Mitchell (1956) attempted to separate the males on the basis of slightly different clypeal configuration and differences in the lengths of the first and second flagellar segments.

The outline of the clypeal margin is variable in males of *C. odontostoma,* and I have seen a series of males of this species in which the configuration matches that described for *C. browni.* The relative lengths of the first and second flagellar segments are useful, though the difference between the two species is not as described by Mitchell. It is true that in *C. odontostoma* the second segment is about three times as long as the first (range: 2.75–3.00). It is not true, however, that in *C. browni* the second segment is four times as long as the minimum length of the first. In the specimens I have been able to examine, the range is second segment 3.33 to 3.67 times longer than the minimum length of the first segment.

In addition to the difference in the flagellar segments, the top of the head is smooth and shiny between punctures in *C. browni* males; the interspaces are polished and without traces of tessellation. Tessellation is conspicuous in the interspaces in *C. odontostoma,* and the integument is only slightly shiny. Much the same is true of the mesoscutum, and, in general, *C. browni* is shinier than *C. odontostoma.*

Whereas males of both species possess flocculent hairs laterad on the pronotal collar, in *C. browni* these hairs form a conspicuous, compact cluster, rather than being well spaced as in *C. odontostoma.* For further description of *C. browni,* see Mitchell (1934).

This is one of the less commonly collected species of *Chalicodoma* in the western deserts. There are only a few previous records: two from Arizona (Yuma, the type locality, and Santa Rita Mountains), two from California (San Felipe Valley and Magnesia Canyon), and one from Baja California, Mexico (Bahia de Los Angeles).

The following are new records for *C. browni.* UNITED STATES, *ARIZONA,* Coconino Co.: 1 ♀, 6 mi S Sedona, 29 July 1977 (J.D. Pinto; UCR). Gila Co.: 1 ♀, Salt River Canyon, 7 June 1971 (G.W. Apperson; BBSL). La Paz Co.: 1 ♀, 18 mi SE Parker, 7 May 1966 (S.A. Gorodenski, J.M. Davidson, M.A. Cazier; ARSU), on *Asclepias erosa.* Yavapai Co.: 1 ♂, 5 mi N Yarnell, 22 June 1971 (G. Bohart and P. Torchio; BBSL), on *Eriodictyon angustifolium;* 1 ♂, Yarnell, 22 June 1971 (G. Bohart and P. Torchio; BBSL), on *Melilotus alba;* 5 ♀♀, 2♂♂, same locality, 10 July 1959 (LACM). *CALIFORNIA,* Imperial Co.: 1 ♂, Glamis, 26 Apr. 1972 (J.L. Neff, No. 63875; LACM), on *Asclepias subulata.* Inyo Co.: 14 ♀♀, 4 ♂♂, Tecopa, 8 June 1983 (K.W. Cooper; KWC), on *Prosopis.* Riverside Co.: 1 ♀, Blythe, 24 May 1971 (M.S. Wasbauer; CDFA), on *Cercidium;* 5 ♀♀, 1 ♂, 2 mi NW Blythe, 31 Apr. 1972 (F. Parker, P. Torchio, G. Bohart; BBSL). San Bernardino Co.: 2 ♂♂, Twentynine Palms, 14 May 1981 and 18 May 1983 (K.W. Cooper; KWC), on *Prosopis.* San Diego Co.: 1 ♀, Jacumba, 29 June 1963 (T. Boton; BBSL); 5 ♀♀, 1 ♂, 6 mi E Banner, 13 July 1963 (W.C. Reische; UCD); 19 ♀♀, same except (J.D. Birchim; CAS); 1 ♀, Scissors Crossing, 4 July 1956 (L.A. Stange; LACM). *NEVADA,* Clark Co.: 1 ♂, Mesquite, Mar. 1953 (G.E. Bohart, BBSL), "from tubular nests"; 2 ♀♀, 1 ♂, Glendale, 27 Apr. 1973 (F. Parker and P. Torchio; BBSL) , on *Sphaeralcea* (1 ♀) and *Acacia* (1 ♀, 1 ♂). MEXICO, *BAJA CALIFORNIA:* 1 ♀, Las Arrastras de Arriola, 29 June 1961 (R. Maynard and J. Honey; LACM); 1 ♀, 13 km NW Rosarito, 9 Sept. 1977 (R.R. Snelling; LACM); 2 ♀♀, 14 km S Rosarito, 9 Sept. 1977 (E.M. Fisher and R. L. Westcott; CAS).

Known plant associations for *C. browni* consist of the following. ASCLEPIADACEAE: *Asclepias* sp. BORAGINACEAE: *Plagiobothrys* sp. CACTACEAE: *Opuntia* sp. FABACEAE: *Acacia* sp., *A. greggii, Dalea* sp. (*Psorothamnus*?), *Melilotus alba, Prosopis glandulosa, P. g.* var. *torreyana.* FRANKENIACEAE: *Frankenia palmeri.* HYDROPHYLLACEAE: *Eriodictyon angustifolium.* KOEBERLINIACEAE: *Canotia* sp. TAMARICACEAE: *Tamarix pentandra.*

## *Chalicodoma* (*Chelostomoides*) *chilopsidis* (Cockerell)

Figures 59, 60

*Lithurgus oblongus* W. Fox, 1893:20; ♀. Preoccupied.

*Megachile chilopsidis* Cockerell, 1900:17; ♀.

*Megachile longula* W. Fox, 1902:137. New name for *L. oblongus* W. Fox.

*Megachile pratti* Cockerell, 1913:541; ♂.

*Megachile* (*Chelostomoides*) *chilopsidis:* Mitchell, 1956:126–130, 135, 136; ♀♂.

Fox's original name for this species remains a secondary homonym, even after having been transferred from *Megachile* (where it was preoccupied by *M. oblonga* F. Smith, 1879) to *Chalicodoma;* the primary homonymic species is also a *Chalicodoma* (Michener, 1965). For further description of this species, see Mitchell (1956).

Female clypeal configuration (Figs. 52, 53) is diagnostic for this sex. Males are less easily separated from others without both a ventral mandibular process and a median clypeal tubercle. Among these species, however, the presence of conspicuous, dark hairs interspersed among the pale hairs of the clypeus is diagnostic for *C. chilopsidis* males. Also useful in recognizing males is the conspicuously bidentate carina of tergum 6 and the polished integument between the punctures of the vertex and mesosomal dorsum.

From the superficially similar *C. adelphodonta, C. chilopsidis* males are separable by the greater interspace between the teeth of the carina of tergum 6 and by the second flagellar segment being about 2.5 times longer than the minimum length of the first (less than twice as long in *C. adelphodonta*); *C. adelphodonta* males lack anterior patches of flocculent hairs on the mesoscutum. Another similar species is *C. discorhina,* the male of which has a wholly flat clypeus, rather than convex over the basal one-half or more.

This is a Creosote Scrub desert species, ranging from western Texas to southern California and across the adjacent northern states in Mexico. It is a primarily vernal bee, mostly flying from April to June.

Floral visits for nectar and/or pollen are recorded within 25 plant genera representing 11 families, Fabaceae predominating. The known floral records, for nectar and/or pollen, for *C. chilopsidis* consist of the following. ASTERACEAE: *Cirsium* sp., *Encelia farinosa, Helianthus* sp., *H. annuus, Senecio* sp., *Verbesina encelioides.* BIGNONIACEAE: *Chilopsis linearis.* BORAGINACEAE: *Heliotropium curassavicum.* FABACEAE: *Acacia greggii, Cercidium floridum, C. microphyllum, C. peninsulare, Hoffmannseggia* sp., *Medicago sativa, Melilotus* sp., *Mimosa* sp., *Olneya tesota, Parkinsonia aculeata, Prosopis glandulosa, P. g.* var. *torreyana, P. velutina, Psorothamnus arborescens* var. *simplifolius, P. californica, P. spinosus.* HYDROPHYLLACEAE: *Phacelia ramosissima.* LAMIACEAE: *Hyptis emoryi, Marrubium vulgare.* MALVACEAE: *Sphaeralcea* sp. ROSACEAE: *Vauguelinia* sp. SAPINDACEAE: *Sapindus* sp., *S. saponaria* var. *drummondi.* SCROPHULARIACEAE: *Cordylanthus littoralis.* ZYGOPHYLLACEAE: *Larrea tridentata.*

## *Chalicodoma* (*Chelostomoides*) *discorhina* (Cockerell)

Figures 63, 64

*Megachile discorhina* Cockerell, 1924:549; ♀.
*Megachile* (*Chelostomoides*) *discorhina:* Mitchell, 1934:384, 404–405; ♀. Mitchell, 1956:131, 135, 136; ♀♂.

A Creosote Scrub desert species, *C. discorhina* ranges from New Mexico to southern California. Although I have seen no specimens from the state of Sonora, Mexico, *C. discorhina* surely is present there. In Lower California, it is known from both Baja California and Baja California Sur.

As usual in *Chelostomoides,* the bizarre clypeal and mandibular modifications of females of this species (Figs. 63, 64) are distinctive. The male most closely resembles that of *C. chilopsidis* but differs immediately in the wholly flat clypeus and the lack of dark hairs among the whitish clypeal pubescence. There is also a similarity to *C. adelphodonta,* a species that lacks patches of flocculent hairs at the anterior portion of the mesoscutum. For a complete description of this species, see Mitchell (1934).

Floral visits, for nectar and/or pollen, have been recorded for 18 plant genera, representing eight families; most records are within the family Fabaceae. Hurd and Linsley (1975) noted that "... females commonly take pollen from *Larrea* ..." and "also visit *Cercidium* and, to a lesser extent, *Acacia* and *Prosopis.*" Known floral associations for *C. discorhina* are as follows. ASTERACEAE: *Baileya* sp., *Encelia farinosa, Senecio* sp. BRASSICACEAE: *Lepidium* sp. CAPPARIDACEAE: *Isomeris arborea.* FABACEAE: *Acacia greggii, Cercidium* sp., *C. floridum, C. microphyllum, C. peninsulare, Coursetia* sp., *Hoffmannseggia microphylla, Medicago sativa, Melilotus* sp., *Parkinsonia aculeata, Prosopis glandulosa, P. g.* var. *torreyanum, Psorothamnus schottii.* LAMIACEAE: *Hyptis emoryi.* MALVACEAE: *Sphaeralcea* sp., *S. ambigua.* TAMARICACEAE: *Tamarix gallica.* ZYGOPHYLLACEAE: *Larrea tridentata.*

In southern California, the flight period is late March and April, and in Arizona is April through early June.

The parasitoid *Leucospis affinis* Say (Leucospidae) has been reared from a nest of *C. discorhina* (Hurd, 1979).

## *Chalicodoma* (*Chelostomoides*) *lobatifrons* (Cockerell)

Figures 9, 65, 66

*Megachile lobatifrons* Cockerell, 1924:547; ♀♂.
*Megachile* (*Chelostomoides*) *lobatifrons:* Mitchell, 1937: 384, 385, 406–408; ♀♂. Mitchell, 1956:132, 134, 136; ♀♂.

Females of *C. lobatifrons* are recognizable by the presence of a dorsal mandibular process and the distinctive clypeal form (Figs. 65, 66). The male is readily identifiable by the unique, very narrow process of the carina of tergum 6 (Fig. 9). For further description, see Mitchell (1937, 1956).

This is a Creosote Scrub desert species ranging from New Mexico to southern California and adjacent areas of Mexico. Floral records are few. Known pollen and/or nectar sources include plants of 10 genera, representing six families.

Following are the known floral associations of *C. lobatifrons.* ASTERACEAE: *Viguera longifolia.* CAPPARIDACEAE: *Wislizenia refracta.* EUPHORBIACEAE: *Euphorbia albomarginata..* FABACEAE: *Acacia greggii, Cercidium* sp., *Olneya tesota, Prosopis glandulosa* var. *torreyana, P. pubescens, P. velutina, Psorothamnus emoryi.* POLYGONACEAE: *Eriogonum fasciculatum, E. inflatum, E. trichopes.* ZYGOPHYLLACEAE: *Larrea tridentata.*

Available records indicate a flight period extending from late May to early July. A female collected at Salton Sea State Park, Imperial Co., California, was provisioning a nest in a gall on *Encelia*.

### *Chalicodoma* (*Chelostomoides*) *odontostoma* (Cockerell)

Figures 3, 6, 56

*Megachile odontostoma* Cockerell, 1924:550; ♀.
*Megachile* (*Chelostomoides*) *duplexa* Mitchell, 1934:353; ♂. Mitchell, 1037:385, 411; ♂.
*Megachile* (Chelostomoides) *odontostoma:* Mitchell, 1937:383; ♀. Mitchell, 1956:131, 134, 136; ♀♂.

The prominent, narrow, acute lateral clypeal lobes of the female are distinctive (Fig. 56). The male, among those lacking a ventral mandibular process, may be recognized by the weakly bilobate carina of tergum 6 (Fig. 6), the lack of a median tubercle on the clypeal margin (Fig. 3), the presence of flocculent patches on the mesoscutum, and the distinctly tessellate surface of the vertex. See Mitchell (1937, 1956) for further description.

This species ranges through the Creosote Scrub desert, from western Texas to southern California and in adjacent areas of northern Mexico. Although there are no substantiating records, it probably occurs in southern Nevada.

Floral records are few but include 21 genera in nine families. Following are the known floral associations for *C. odontostoma.* ASCLEPIADACEAE: *Asclepias* sp., *A. erosa.* ASTERACEAE: *Aster* sp., *Baileya* sp., *Chaenactis stevioides, Encelia* sp., *E. farinosa, Geraea canescens, Helianthus* sp., *Palafoxia linearis, Senecio* sp., *Verbesina encelioides.* BORAGINACEAE: *Heliotropium curassavicum.* BRASSICACEAE: *Lepidium* sp., *Lesquerella* sp. FABACEAE: *Acacia greggii, Cercidium floridum, Medicago sativa, Melilotus* sp., *Prosopis glandulosa, P. g.* var. *torreyanum, P. velutina.* HYDROPHYLLACEAE: *Phacelia* sp. MALVACEAE: *Sphaeralcea* sp. TAMARICACEAE: *Tamarix gallica.*

Flight records extend from late March to mid-May.

### *Chalicodoma* (*Chelostomoides*) *rugifrons* (F. Smith)

*Chelostoma rugifrons* F. Smith, 1854:220; ♀.
*Chelostomoides rugifrons:* Cockerell, 1904:301; ♀.
*Megachile rufimanus* Robertson, 1891:65; ♀♂.
*Megachile* (*Chelostomoides*) *rugifrons:* Mitchell, 1937:384, 385, 412–414; ♀♂. Mitchell, 1956:135, 137; ♀♂.

This is the only eastern species in which the female clypeus is modified and the mandibles are slender and tridentate. The male lacks a ventral mandibular process, the carina of tergum 6 is weakly bilobate, and the ocellocular distance is distinctly shorter than the ocelloccipital distance. In both sexes, the punctures of the vertex are unusually coarse. For further description, see Mitchell (1937, 1956).

The range of *C. rugifrons* extends from Virginia and Michigan south to Florida and westward to Nebraska, Kansas, Oklahoma, and Texas.

Floral records for nectar and/or pollen include plants of 14 genera, belonging to 10 families. Known floral associations of *C. rugifrons* are as follows. APOCYNACEAE: *Apocynum* sp. ASTERACEAE: *Coreopsis* sp., *Erigeron* sp. ERICACEAE: *Vaccinium* sp. FABACEAE: *Lotus* sp., *Psoralea* sp., *Tephrosia* sp. HYPERICACEAE: *Hypericum* sp. LAMIACEAE: *Blephilia* sp., *Nepeta* sp. LOBELIACEAE: *Lobelia* sp. PONTEDERIACEAE: *Pontederia* sp. SCROPHULARIACEAE: *Veronicastrum virginicum.* VERBENACEAE: *Verbena* sp.

According to Mitchell (1962), the flight period is April to July.

## Groups VII–X

The following four groups represent species that do not appear to belong to any of the preceding five groups. As a whole they share the following suite of characters: male mandible slender, tridentate, and without ventral process; hypostomal acetabulum absent; male procoxa without apical process; male protarsal segments slender and basal segments densely setose on inner side; female clypeus variously modified; female tergum 6 without preapical groove; mesoscutum of both sexes without notaular patches or transverse anterior band of flocculent hairs.

## Group VII (*manni* Group)

This group includes a single, poorly known species, *C. manni* (Mitchell), known only from a few specimens from southern Arizona. The female clypeus is beveled and transversely bowed across the basal facet, the lower facet is oblique and simple; the apical margin is fully exposed, straight, and without denticles. The mandible is stout and quadridentate (or weakly quinquedentate). Tergum 6 has a transverse preapical carina, but it is not preceded by a groove as in female members of Group I (*exilis* group).

The presumed male of *C. manni* has a median denticle on the clypeal margin and larger, sublateral denticles. Tergum 6 has a low, obsolete carina that is weakly emarginate in the middle, and the apical margin is without lateral or submedian teeth.

### *Chalicodoma* (*Chelostomoides*) *manni* (Mitchell)

Figure 53

*Megachile* (*Chelostomoides*) *manni* Mitchell, 1934: 355; ♀♂. Mitchell, 1937:409; ♀♂. Mitchell, 1956: 134, 136; ♀♂.
*Chalicodoma* (*Chelostomoides*) *manni:* Hurd, 1979: 2075.

This rare species is known only from a few specimens from the Huachuca Mountains of southern Arizona. See Mitchell (1934, 1937, 1956) for descriptions of this species.

## Group VIII (*texensis* Group)

**GROUP CHARACTERS.** Female clypeus with conical preapical process and anterior margin with prominent submedian tubercles (Figs. 54, 67); male clypeal margin without denticles or tubercles; male frons dull and contiguously punctate; mesoscutum of both sexes shiny between uniformly subcontiguous punctures.

**INCLUDED SPECIES.** *Chalicodoma axyx*, n. sp., and *C. texensis* (Mitchell).

One species (*C. texensis*) ranges from southern Texas and central Mexico south to Costa Rica; in Mexico it ranges west to the Pacific Coast. The other species is presently known only from Costa Rica.

## *Chalicodoma* (*Chelostomoides*) *axyx*, new species

Figures 19, 21, 25, 27, 33–35, 67, 68

### DIAGNOSIS

Female mandible long and slender, with three apical teeth and with prominent conical, preapical process, the margin between the conical process and the innermost of the apical teeth deeply concave and much shorter than the apical width of the mandible (Fig. 21); otherwise similar to female of *C. texensis*, but legs usually ferruginous or light reddish brown. Male similar to that of *C. texensis*, but legs ferruginous; pro- and mesotarsi with dense fringe of white hairs along posterior margin of basitarsus that are longer than their segment.

### DESCRIPTION

**FEMALE.** Measurements (mm): HOLOTYPE HW 3.23; HL 2.50; WL 6.7; TL 10.2. Paratypes: HW 2.87–3.49; HL 2.36–2.72; WL 5.7–7.2; TL 8.9–12.0.

Generally similar to female of *C. texensis*, as described below, but with postmedian tooth of upper margin of mandible prominent and margin between it and innermost apical tooth distinctly concave and shorter than apical width of mandible (Fig. 21). Clypeal structure as in *C. texensis*, but disc rugosopunctate, with narrow, shiny, impunctate area across basal margin. Supraclypeal area weakly elevated and with coarser, contiguous punctures. Frons and vertex similar to those areas of *C. texensis* but frons rugosopunctate. Gena, in profile, about three-fourths as wide as eye, shiny between subcontiguous fine punctures. Pedicel about twice longer than first flagellar segment and a little less than twice longer than second. Interocellar and ocellocular distances subequal and greater than ocelloccipital distance.

Mesosoma, metasoma, and pubescence as in *C. texensis.*

Color of head and body blackish brown; mandible dark reddish near apex; scape, pedicel, and upper side of flagellum brownish, underside of flagellum lighter. Tegula transparent yellowish red. Femora and tibiae light ferruginous; tarsal segments duskier.

**MALE.** Measurements (mm): Allotype HW 2.86; HL 2.29; WL 5.9; TL 9.3. Paratypes: HW 2.71–3.33; HL 2.05–2.67; WL 5.5–6.7; TL 7.5–10.4.

Head 1.25–1.32 times as broad as long; eyes weakly convergent below, upper interorbital distance about 1.1 times lower interorbital distance; in frontal view, preoccipital margin arcuately produced above ocelli by less than transverse diameter of anterior ocellus. Mandible as described for *C. texensis*. Labrum as described for *C. texensis*, but impunctate area limited to basal one-fourth to one-third. Clypeus as described for *C. texensis* but very weakly produced in middle, and median impunctate line weak or absent. Supraclypeal area, frons, vertex, preocciput, and gena as described for *C. texensis*. Pedicel and first two flagellar segments as described for *C. texensis*. Interocellar distance greater than ocellocular distance, each distinctly greater than ocelloccipital distance.

Mesoscutal interspaces moderately shiny, distinctly tessellate, punctures subcontiguous to dense; mesosoma otherwise as described for *C. texensis*.

Legs as described for *C. texensis*, but mesobasitarsal fringe long (Fig. 25).

Metasoma as described for *C. texensis*, but carina of tergum 6 low and shallowly emarginate in middle; hidden sterna and genitalia (Figs. 27, 33–35).

Pilosity as described for *C. texensis*, but posterior margins of pro- and mesobasitarsi with sparse fringe of yellowish hairs that are conspicuously longer than the segment.

Color as described for *C. texensis*, but femora and tibiae ferruginous.

### TYPE MATERIAL

Holotype female: Hacienda Comelco, 24 km NW Cañas, Guanacaste, COSTA RICA, 59 m elev., 16 Feb. 1972 (E.R. Heithaus, no. 18451), on flowers of *Andira inermis*, 1200–1215 hr. Allotype, same locality, collector (no. 19013), and host plant, 6 Mar. 1972, 1045–1120 hr. Paratypes (all Guanacaste Province, COSTA RICA): 44 ♀♀, 3 ♂♂, same locality and collector as holotype, 12 Feb. 1972 (7 ♀♀, 3 ♂♂, on *Caesalpinia eriostachys*), 14 Feb. 1972 (2 ♀♀, on *C. eriostachys*), 16 Feb. 1972. (2 ♀♀, on *C. eriostachys*), 6 Mar. 1972 (7 ♀♀, on *A. inermis*), and 9 Mar (26 ♀♀, on *A. inermis*); 6 ♀♀, 7 km N Cañas, 15 Feb. 1966 (D.H. Janzen), on flowers of *Gliricidia sepium;* 4 ♀♀, 2 mi S Liberia, 2 Mar. 1973, on *A. inermis*, 1 ♀, 29 Dec. 1972, on *C. eriostachys*), and 1 ♀, 30 Dec. 1972, on *Myrospermum fructescens* (all G.W. Frankie); Liberia, 15–16 Feb. 1972 (82 ♀♀, 13 ♂♂, on *A. inermis*), 23–26 Feb. 1972 (50

♀♀, 2 ♂♂, on *A. inermis*, 1 ♀, on *Dalbergia retusa*, 1 ♀, on *Tabebuia rosea*), 1 Mar. 1972 (5 ♀♀, on *A. inermis*) (all P.A. Opler); Hacienda Comelco, 8 km NW Bagaces, 8–9 Jan. 1973 (3 ♂♂, on *Simaruba glauca*), 22 Jan. 1972 (1 ♂, on *G. sepium*), 24–25 Jan. 1972 (2 ♂♂, on *Byrsonima* sp.), 29 Jan. 1972 (3 ♂♂, on *Securidaca sylvestris*), 10 Feb. 1972 (17 ♀♀, on *Pterocarpus rohrii*), 6 Mar. 1971 (1 ♀, on *D. retusa*), 25 Mar. 1972 (12 ♀♀, on *Lonchocarpus costaricensis*), 17 Apr. 1971 (1 ♀, on *D. retusa*), 25 Nov. 1972 (5 ♀♀, 5 ♂♂, on *A. inermis*), 28 Dec. 1972 (2 ♂♂, on *C. eriostachys*) (all P.A. Opler); Bagaces, 4 Mar. 1974 (P.A. Opler), 2 ♀♀, on *A. inermis;* Finca La Pacifica, 4 mi NW Cañas, 25–30 Jan. 1972 (2 ♀♀, 1 ♂, on *M. fructescens*), 12 Feb. 1972 (1 ♂, on *Inga* sp.), 14 Mar. 1973 (3 ♀♀, 3 ♂♂, on *D. retusa*) (all P.A. Opler); 1 km W Río Blanco, 15 Apr. 1971 (P.A. Opler), 3 ♀♀, on *D. retusa*. Holotype and allotype in LACM; paratypes in LACM, TAMU, UCB, UKAN, and USNM.

## ETYMOLOGY

The specific name is an arbitrary combination.

## DISCUSSION

There is little variation in the long series of paratypes studied; the differences in size are noted above in the description. The form of the female clypeal apex is unique to this species and *C. texensis;* in *C. axyx* the clypeal disc is much more closely punctate, usually appearing rugosopunctate, than in *C. texensis*. The most important difference between the females is the much stronger submedian angulation of the upper margin of the mandible in *C. axyx*, with the deep concavity following it distinctly shorter than the apical width of the mandible (Fig. 21); in *C. texensis* the concavity is shallow and is longer than the apical width of the mandible (Fig. 22). While both sexes of *C. axyx* generally have conspicuously ferruginous legs, a few have the legs brownish infuscate, and this character must be used with caution. Males of *C. axyx* differ consistently from those of *C. texensis* by the dense fringe of long, plumose hairs on the pro- and mesobasitarsi; most of the hairs of the fringe are distinctly longer than the basitarsus from which they arise.

The floral records presently available for *C. axyx* represent five families. BIGNONIACEAE: *Tabebuia rosea.* FABACEAE: *Andira inermis, Caesalpinia eriostachys, Dalbergia retusa, Gliricidia sepium, Inga* sp., *Lonchocarpus costaricensis, Myrospermum fructescens, Pterocarpus rohrii.* MALPIGHIACEAE: *Byrsonima* sp. POLYGALACEAE: *Securidaca sylvestris*. SIMARUBACEAE: *Simaruba glauca*.

## *Chalicodoma* (*Chelostomoides*) *texensis* (Mitchell)

Figures 10, 22, 26, 37, 54

*Megachile* (*Chelostomoides*) *texensis* Mitchell, 1956:132–133; ♀.

This species was described from a single female collected at Southmost, Cameron Co., Texas; the type is in the USNM, and I have examined it. Although *C. texensis* barely enters the United States, it is widely distributed in Mexico and extends south to Costa Rica.

The male has not been previously described and both sexes are redescribed to provide a comparative basis for the very similar *C. axyx*, described above. Costa Rican females differ from those of Mexico (and the type) in having larger and stouter submedian clypeal tubercles and the process of the disc blunter (Fig. 54). Males from the two areas are more similar, but those from Costa Rica are, on the average, more densely punctate on the frons and vertex.

## DESCRIPTION

**FEMALE.** Measurements (mm): HW 2.92–3.28; HL 2.31–2.62; WL 6.0–6.5; TL 9.0–10.5.

Head (Fig. 54) about 1.3 times as broad as long; inner eye margins weakly divergent below, upper interorbital distance about 0.8 times lower interorbital distance; in frontal view, vertex strongly elevated above eyes and ocelli. Mandible slender, with three distinct apical teeth and an obscure denticle in second interspace; submedian angulation of upper margin weak, margin between it and third tooth shallowly concave and about as long as apical width of mandible (Fig. 22). Sides of labrum mostly subparallel, narrowed preapically; apical margin transverse; with median preapical seta-pit with cluster of long, reddish setae and small pit on either side with a single long seta arising from each. Clypeal margin broadly concave, with a pair of prominent submedian denticles; disc elevated along midline, with large conoid projection above and between submedian denticles of margin (Fig. 57); disc shiny between subcontiguous to contiguous coarse punctures, impunctate in middle. Supraclypeal area slightly elevated toward base of clypeus, punctation similar to that of clypeus. Punctation of frons, vertex, preocciput, and gena as in male but interspaces shiny. Pedicel about 1.5 times longer than either first or second flagellar segments. Interocellar distance greater than ocellocular distance; ocellocular distance equal to, or a little greater than, ocelloccipital distance.

Mesoscutum and scutellum as in male but interspaces shiny; mesepisternum shiny between subcontiguous to dense, moderate punctures; metepisternum and side of propodeum moderately shiny between moderate, subcontiguous punctures; remainder of propodeum as in male.

Disc of first two terga moderately shiny between fine, subcontiguous to dense punctures; third and fourth terga similar but punctures less distinct, more separated; punctures of fifth tergum a little coarser, dense; sixth tergum finely, subcontiguously punctate, without preapical groove.

Pubescence about as in other *Chelostomoides*.

Clypeal hairs sparse, a few at sides somewhat brownish; supraclypeal area with a few brownish hairs interspersed among usual white hairs; hairs brownish on vertex and occiput and with some scattered brownish hairs on mesoscutum and scutellum; pronotal collar and mesoscutum without definite patches of flocculent hairs; first five terga with apical fringes of short, flocculent, appressed, white hairs; second and third terga with pubescent fasciae in basal gradular depression; discs of second to fifth terga with blackish pubescence only; sixth tergum wholly dark pubescent; scopa slightly yellowish, except blackish on apical segment.

**MALE.** Measurements (mm): HW 2.76–3.29; HL 2.14–2.52; WL 5.8–6.4; TL 8.0–10.5.

Head about 1.3 times as broad as long; inner eye margins weakly convergent below, upper interorbital distance about 1.1 times lower interorbital distance; in frontal view preoccipital margin arcuately produced above ocelli by less than transverse diameter of anterior ocellus. Mandible without ventral process; apex tridentate, inner tooth on same plane as first and second teeth. Lateral margins of labrum slightly convergent apicad, apex truncate, disc shiny, nearly impunctate on basal one-half or less, integument slightly roughened between fine, dense punctures on distal one-half or more. Clypeus weakly convex, apical margin weakly produced in middle and shallowly emarginate, shorter than length of lateral margin between process and angle at eye margin; punctures of disc contiguous, fine to moderate over most of disc, becoming fine to minute toward apical margin; median impunctate line present but often weak, interspaces smooth and shiny. Supraclypeal area and frons slightly shiny, variably finely rugosopunctate to contiguously punctate; vertex and preocciput slightly shiny between fine contiguous to subcontiguous punctures. Gena about half as wide as eye in profile, shiny between fine contiguous to subcontiguous punctures. Pedicel about as long as first flagellar segment; first flagellar segment distinctly broader than long and about one-half as long as second flagellar segment. Interocellar and ocellocular distances subequal and longer than ocelloccipital distance.

Mesoscutum and scutellum moderately shiny and weakly tessellate between subcontiguous fine to moderate punctures; metanotum less shiny, punctures fine and close to dense; mesepisternal punctation similar to mesoscutum but interspaces a little less shiny; side of propodeum slightly shiny and roughened between obscure, contiguous to subcontiguous, fine punctures.

Anterior face of procoxa with abundant long, erect, plumose hairs; without apical process. Probasitarsus slender and simple, without mastigion; second protarsal segment about one-third as long as first, asymmetrical; last protarsal segment distinctly shorter than first.

Metasomal terga 1–4 shiny, but not polished between very irregularly spaced fine to moderate punctures; tergum 5 similar but subcontiguously punctate; tergum 6 similar but contiguously punctate, carina bilobate, apical margin without lateral or submedian teeth or angles. Exposed sterna slightly to moderately shiny between mostly subcontiguous, fine to moderate punctures.

Pilosity erect, mostly white and conspicuously plumose; long, brownish to blackish hairs abundant on clypeus, frons and vertex, posterior one-third of mesoscutum and scutellum. Discs of metasomal terga 2–5 with sparse, very short, suberect brownish hairs; tergum 6 with short, appressed, plumose, white hairs across base and in depression basad of transverse carina; sternum 3 mostly concealed by dense, appressed, white, plumose hairs. Hairs along posterior margins of pro- and mesobasitarsi (Fig. 26) sparse and not forming a definite fringe.

Color of head and body blackish, but tergum 6 and sterna 2–3 mostly light ferruginous; appendages brownish, underside of flagellum and tarsi ferruginous. Wings clear, veins and stigma light to medium brown.

In addition to the type, I have seen the following specimens of *C. texensis*. UNITED STATES, *TEXAS:* 3 ♂♂, Southmost, Cameron Co., 27 Mar. 1951 (L.D. Beamer; UKAN), on *Agastache breviflora.* MEXICO, *CHIHUAHUA:* 3 ♂♂, Santo Niño, 10 Aug. 1968 (T.C. Sears, R.C. Gardner, C.S. Glaser; UCD). *JALISCO:* 1 ♀, Estación Biologia de "Chamela," 9 Apr. 1982 (S.H. Bullock No. 932; LACM); 3 ♀♀, same locality and collector, 12 and 19 May 1980. *PUEBLA:* 1 ♀, 4 mi NW Choix, 17 July 1968 (T.C. Sears, R.C. Gardner, C.S. Glaser, UCD); 1 ♀, 1 ♂, same locality and collectors, 31 Aug. 1968. *SONORA:* 2 ♂♂, 5 mi E Navojoa, 2 Aug. 1960 (Arnaud, Ross, Rentz; CAS); 1 ♂, Río Cuchuhaqui, 7 mi S Alamos, 25 July–7 Aug. 1953 (F.S. Truxal; LACM). *VERA CRUZ:* 2 ♀♀, Eypantla, 12 Mar. 1981 (J.L. Neff; NEFF), at nests in beetle burrows in post of ramada. *YUCATÁN:* 1 ♀, Uxmal ruins, 14 Feb. 1987 (C.D. Michener; UKAN); 1 ♂, Koban, 25 km SW Ticul, 14 Feb. 1987 (C.D. Michener; UKAN); 5 ♀♀, 4 ♂♂, Yodronot, 16 Feb. 1987 (C.D. Michener; UKAN). COSTA RICA, *GUANACASTE:* 1 ♀, 8 ♂♂, Finca La Pacifica, 4 km NW Cañas, 14 Mar. 1973 (P.A. Opler; UCB), on *Dalbergia retusa;* 1 ♀, 4 mi N Cañas, 15 Feb. 1966 (D.H. Janzen; UKAN), on *Gliricidia sepium;* 1 ♀, 1 ♂, Hacienda Comelco, 24 km NW Cañas, 14 Feb. 1972 (E.R. Heithaus; LACM), on *Caesalpinia eriostachys*, 1015 hr; 3 ♀♀, same locality and collector, 6 Mar. 1972, on *Andira inermis*, 1045–1120 hr; 2 ♀♀, same locality and collector, 9 Mar. 1972, on *A. inermis*, 0745–0815 hr; 1 ♂, Hacienda Comelco, 8 km NW Bagaces, 22 Jan. 1972 (P.A. Opler; UCB), on *G. sepium;* 1 ♀, 1 ♂, same locality and collector, 25 Mar. 1972, on *Lonchocarpus costaricensis;* 5 ♀♀, 1 ♂, same locality and collector, 28 Dec. 1972, on *C. eriostachys;* 1 ♀, Bagaces, 4 Mar. 1974 (P.A. Opler; UCB), on *A. inermis;* 1 ♀, Río Blanco, 15 Apr. 1971 (P.A. Opler; UCB), on *A. inermis;* 3 ♀♀, 5♂♂, same locality and collector, 23–26 Feb. 1972, on *A. inermis;* 2 ♂♂, same locality and collector, 1

Mar. 1972, on *A. inermis;* 1 ♀, 2 mi N Liberia, 2 Mar. 1972 (G.W. Frankie; TAMU), on *A. inermis*, 1330-1345 hr.

The type female was reportedly collected on flowers of *Parkinsonia* sp.; all available floral records are from the family Fabaceae.

## Group IX (*adelphodonta* Group)

This group includes only *C. adelphodonta*, a species known only from southern Arizona and from Lower California, Mexico. The female is easily recognized by the flat clypeus, the apical margin of which is broadly excised on either side of a broad, apically tridentate, median lobe (Fig. 55). The male is similar to those of Group V males, but the carina of tergum 6 is bidentate, with the teeth close together, the clypeus and frons are shiny between well-defined, subcontiguous punctures, the mesoscutum lacks flocculent hair patches, and the first flagellar segment is about one-half as long as the second.

### *Chalicodoma* (*Chelostomoides*) *adelphodonta* (Cockerell)

Figures 11, 55

*Megachile adelphodonta* Cockerell, 1924:548; ♂.
*Megachile (Chelostomoides) tucsonensis* Mitchell, 1956:133; ♀.

Cockerell (1924) described *M. adelphodonta* from a single male collected at Guadalupe Point, Bahia Concepcion, Baja California Sur, Mexico. The type locality of *M. tucsonensis* is Tucson, Arizona, and is also based on a single specimen. A number of specimens of both sexes are available and appear to confirm the above synonymy by Hurd (1979). For further description of *C. adelphodonta*, see Mitchell (1956).

In addition to the types of *M. adelphodonta* and *M. tucsonensis*, I have seen the following specimens. UNITED STATES, *ARIZONA:* 1 ♀, 1 mi N Portal, Cochise Co., 23–24 Aug. 1973 (E.G. and J.M. Linsley; UCB), on *Larrea divaricata*, 1030–1059 hr; 1 ♀, Sycamore Canyon, near Ruby, Santa Cruz Co., 16–17 Aug. 1961 (F. Werner and J. Bequaert; UNAR); 1 ♀, 3 mi W Oracle, Pima Co., 12 June 1961 (Werner, Bequaert, and Noller; UNAR); 2 ♂♂, Florida Canyon, Santa Rita Mts., Pima Co., 20 Aug. 1961 (Wargo; UNAR), on Arizona poppy (*Argemone* sp.); 1 ♂ Ruby, Santa Cruz Co., 16 Aug. 1961 (J.C. Bequaert; UNAR); 1 ♀, 1 ♂, 5.5 mi W Peña Blanca, Santa Cruz Co., 17 Aug. 1961 (F. Werner and J. Bequaert; UNAR); 1 ♀, 5 mi S Amado, Santa Cruz Co., 2 Sept. 1977 (E.G. and J.M. Linsley; UCR), taking nectar of *Kallstroemia grandiflora*, 0830–0859 hr. MEXICO, *BAJA CALIFORNIA SUR:* 2 ♂♂, 35 mi N Loreto, 5 Oct. 1975 (R.R. Snelling; LACM), on *Wislizenia refracta;* 1 ♂, 10 km W Ramal Los Naranjos, 26 Aug. 1982 (Faulkner and Brown; SDM). *SONORA:* 1♂, 3 mi NE San Carlos, 22 Mar. 1967 (E.M. Fisher; LACM).

Including the above, known floral data for *C. adelphodonta* consist of the following records. ASTERACEAE: *Helianthus annuus.* CAPPARIDACEAE: *Wislizenia refracta.* FABACEAE: *Dalea albiflora, Prosopis glandulosa* var. *torreyana, Psorothamnus scoparius.* NYCTAGINACEAE: *Allionia* sp. PAPAVERACEAE: *Argemone* sp. ZYGOPHYLLACEAE: *Kallstroemia grandiflora, Larrea divaricata.*

## Group X (*ecplectica* Group)

**GROUP CHARACTERS.** Female clypeus bizarre and gena with secondary carina parallel with hypostomal carina; female without transverse preapical groove on tergum 6. Male unknown.

**INCLUDED SPECIES.** *Chalicodoma ecplectica*, n. sp. The only known species in this group is known only from southern Mexico. The male is unknown.

### *Chalicodoma* (*Chelostomoides*) *ecplectica*, new species

Figures 73, 74

#### DIAGNOSIS

Known from the female only, this species is separable from all known American *Chalicodoma* by the presence of a sharp cariniform ridge parallel to the hypostomal carina. In addition, the head is unusually broad, the eyes are strongly divergent below, and the clypeus is beveled, with the upper lateral lobes projecting as a tooth-like process (Fig. 73) on either side.

#### DESCRIPTION

**FEMALE.** Measurements (mm): Holotype HW 4.03; HL 2.97; WL 8.3; TL 10.0.

Head (Fig. 73) about 1.3 times as broad as long; inner eye margins strongly divergent below, lower interorbital distance about 1.3 times upper interorbital distance and about 1.4 times eye length; in frontal view, vertex greatly elevated above eyes and ocelli. Mandible slender, apical margin tridentate and about one-fourth as long as lower margin. Hypostomal area, laterad of hypostomal carina, with strong, cariniform ridge extending from outer mandibular base to occipital depression and parallel to hypostomal carina, broad interspace slightly concave, smooth and shiny. Labrum broad at base, margins convergent distad. Clypeus protuberant and bifaced (Fig. 74), lower face smooth and shiny, apical margin simple and not covering base of labrum; upper face with middle lobe transverse and slightly emarginate, separated from lateral lobe by shallow emargination, lateral lobe with oblique corniform process; upper face mostly smooth and shiny but with some moderate to coarse, setigerous punctures. Supraclypeal area shiny between fine to moderate, contiguous to subcontiguous punctures. Frons, vertex, and preocciput dull, punctures coarse and contiguous; gena similar but with interspaces shiny between moderate punctures. Pedicel longer than first or second flagellar segments, first broader than long; second flagellar segment about 1.3 times longer than first. Interocellar distance about 1.8 times diameter of anterior ocellus and about 0.6 times ocellocular distance; ocelloccipital distance about 1.1 times ocellocular distance.

Pretegular carina of pronotum not extending entirely across pronotal lobe. Mesoscutum shiny between contiguous to subcontiguous, moderate to very coarse punctures; scutellum similar but punctures more commonly subcontiguous; mesepisternum similar, punctures mostly contiguous in middle, becoming mostly subcontiguous ventrad; metepisternum and side of propodeum contiguously, finely punctate; propodeal triangle rugosopunctate across base, remainder dull and minutely granulose.

Discs of metasomal terga progressively more shiny distad, punctures moderate and contiguous on first, mostly subcontiguous on remaining segments; last tergum dull, contiguously punctate, without preapical groove.

Pubescence about as in other *Chelostomoides* but clypeus with sparse simple hairs only; pronotal collar and front of mesoscutum without dense, flocculent, long hairs; first five metasomal terga with dense apical fasciae of short, plumose hairs; disc of sixth tergum with pale hairs; scopa pale, including that of sixth sternum.

## TYPE MATERIAL

Holotype female: 11.4 mi W Chilpancingo, 7700 ft elev., *GUERRERO*, MEXICO, 31 July 1969 (University of Kansas Mexican Expedition), in Snow Entomological Museum, University of Kansas. Paratype: 1 ♀, 13 km W Chilpancingo, 31 July 1969 (G. Byers, D. Kamm) in LACM.

## ETYMOLOGY

The specific name is derived from the Greek *ekplektikos* (astounding or marvelous) and stresses the bizarre cephalic features of this species.

## DISCUSSION

The unusual cephalic characteristics of *C. ecplectica* will immediately separate this species from all others. Particularly distinctive is the presence of the cariniform ridge bordering the hypostomal area; this feature is unique within *Chelostomoides*. Until a male can be associated with *C. ecplectica* nothing can be said of the relationship of this species to other *Chelostomoides*.

# *Chelostomoidella*, new subgenus

## DIAGNOSIS

Differs from *Chelostomoides*, the only other native North American subgenus of *Chalicodoma*, by the following unique features: mandible with thin, transparent lamella, parallel to surface of trimma and above it (visible only when mandible is fully opened, larger in male) (Figs. 17, 18); male mandible with process of lower margin located basad; male with prominent, suberect, subbasal, spine-like tubercle on ventral surface of procoxa in addition to that at apex; male mesosternum with a submedian pair of sharp, suberect spiniform tubercles behind procoxa; female mandible with outer ridge and secondary ridge strong from base to near teeth, the two ridges only moderately convergent distad, groove between them broad and deep; preapical groove of female sternum 6 very deep, preceded and followed by transverse carinae.

## DESCRIPTION

**FEMALE.** [1] Mandible broad, apical margin much more than one-half as long as lower margin; with four or five teeth, interspaces without beveled cutting edges; outer ridge and secondary ridge both strong, continuous from near base to near apical teeth, groove between them broad, flat; base with thin, transparent, prostrate lamella above trimma (visible only when mandible is fully opened). [2] Clypeus weakly convex, apical margin overhanging base of labrum and broadly, shallowly emarginate in middle, with median tubercle. [3] First flagellar segment shorter than second. [4] Lower genal area simple.

[5] Meso- and metabasitarsi shorter and narrower than corresponding tibiae; tarsal claws simple.

[6] Mesosoma parallel-sided; tergum 6 with very deep preapical groove, basal face, in profile, projecting over groove as cariniform ridge, posterior carina present.

**MALE.** [7] Mandible broad, tridentate, inner tooth larger than middle tooth and approximately perpendicular to outer margin; ventral process basal; base with thin, transparent, prostrate lamella lying over trimma (Figs. 16, 17). [8] First flagellar segment shorter than second.

[9] Procoxa glabrous beneath, with slender, suberect, discal, spine-like process near base, in addition to larger apical process. [10] Protarsal segments 1–3 greatly expanded, anterior margin of first and second segments with deep, longitudinal channel. [11] Meso- and metabasitarsi shorter and narrower than corresponding tibiae; tarsal claws symmetrical.

[12] Carina of tergum 6 (Fig. 13) with a pair of submedian, long, apically truncate spines; posterior margin with lateral and submedian spines long, acute. [13] Sternum 3 with narrow median row of short, fully erect, spine-like setae over distal one-half. [14] Sternum 4 fully retracted, simple. [15] Sternum 5 (Fig. 48) glabrous except for fringe of short, plumose hairs at apicolateral margin; metasternite very large and extended over lateral parts of poststernite as a broad, membranous flap. [16] Sternum 6 (Fig. 49) with a pair of short submedian carinae, ending distally in tooth-like process, their entire length surmounted by closely ranked, erect, compressed setae; at base of distal tooth-like pro-

cess, a double row of closely ranked, compressed setae extending laterad on each side; poststernite present as a large apically emarginate, very delicate lobe, with transverse wrinkles near base and with scattered short, prostrate setae with reflexed apices, and with a row along distal, incurved margin, and laterad with sparse, fine, simple setae. [17] Gonocoxite (Fig. 47) compressed distad, compressed part slightly bent laterad and its inner margin with sparse, long, simple setae. [18] Volsella with long, slender outer lobe, inner angle subtruncate to broadly rounded (Fig. 47). [19] Aedeagus (Fig. 47) distinctly shorter than gonocoxite, largely thin and transparent over distal one-half.

### TYPE-SPECIES

*Megachile* (*Chelostomoides*) *spinotulata* Mitchell, 1934.

### ETYMOLOGY

The name is a diminutive form of *Chelostomoides*.

### DISCUSSION

This subgenus is monobasic; the only species has previously been included within the subgenus *Chelostomoides*. This one species possesses so many unique features, especially in the male, that I am convinced it must be removed from *Chelostomoides*.

Both sexes share many features with the species of *Chelostomoides* but immediately differ in the presence of a thin, transparent lamella overlying a shallow depression at the base of the trimma. This lamella is not visible when the mandibles are closed. Species of *Chelostomoides* lack both the transparent lamella and the depression at the base of the trimma.

The male of *C. spinotulata* is uniquely different from that of *Chelostomoides* in the glabrous, bispinose ventral surface of the procoxa, the presence of mesosternal spines, the median row of coarse setae on the third sternum, the glabrous fifth sternum, and the blunt, spiniform processes of the carina of tergum 6.

Females of *C. spinotulata* are much less bizarre than males of this species but do differ from those of *Chelostomoides* in a few unique characters other than the presence of the trimmal lamella. The outer face of the mandible is similar to that of the broad mandible forms of *Chelostomoides*. But, in such species the outer ridge is low and broad and, while often extending nearly the full length of the mandible, is always somewhat evanescent, or fully interrupted, at some point beyond the basal one-third. The secondary ridge is normally distinct over the basal one-third, and is greatly reduced or absent beyond. The broad interspace between these ridges is usually flat, but very shallow. In *Chelostomoidella* both ridges are strong and complete from the mandible base to the base of the teeth; because of their elevation, the interspace between them is deep.

Although females of some *Chelostomoides* do possess a preapical groove on the sixth tergum, it is marked only distad by a bordering cariniform ridge. When the sixth tergum of *C. spinotulata* is seen in profile, the basal face partially overhangs the groove; the margin of this extended portion is thin and somewhat carina-like; beyond the posterior carina, the segment is strongly convex and descends abruptly to the translucent posterior margin of the segment.

## *Chalicodoma* (*Chelostomoidella*) *spinotulata* (Mitchell)

Figures 13, 16, 17, 47–50

*Megachile* (*Chelostomoides*) *spinotulata* Mitchell, 1934:357–359; ♀♂

*Megachile* (*Chelostomoides*) *subspinotulata* Mitchell, 1934:360–361; ♀. NEW SYNONYMY.

It is now apparent that *C. subspinotulata* is a synonym of *C. spinotulata*. The differences in size, clypeal dentition and mandibular structure noted by Mitchell (1934) at the time of the original descriptions, are fully bridged by the material I have seen. The inner tooth of the mandible may be truncate at the apex, thus resulting in the four-toothed mandible of *C. subspinotulata*. In *C. spinotulata* the inner tooth is deeply emarginate at the apex; the mandible appears to be five-toothed. Most specimens are intermediate in this character, and their assignment to one or the other name becomes ambivalent.

The structure of the apical margin of the clypeus is variable in this species, as it is in the species of *Chelostomoides*. This is especially true of the width and depth of the median emargination and of the size of the median tubercle.

This species ranges from southern California to western Texas. The following records extend the range of *C. spinotulata* into northwestern MEXICO, *BAJA CALIFORNIA SUR:* 1 ♀, Cañon de Zorra, 260 m elev., 11 km W Santiago, 4–5 Sept. 1977 (R.R. Snelling; LACM), on *Parkinsonia aculeata;* 1 ♀, 19 km NW Mulegé, 8 Sept. 1977 (R.R. Snelling; LACM), on *Hoffmanseggia* sp.; 1 ♂, 4 km N Los Barriles, 10 m elev., 4 Sept. 1977 (R.R. Snelling; LACM). *CHIHUAHUA:* 1 ♀, Santa Clara Canyon, 5 mi W Parrita, 1 Sept. 1956 (J.W. MacSwain; UCB).

Floral visits, for nectar and/or pollen, include plants of 30 genera belonging to 18 families. The following are known floral associations of *C. spinotulata,* in addition to those cited above. ASCLEPIADACEAE: *Asclepias erosa.* ASTERACEAE: *Chrysopis fastigiata, Chrysothamnus* sp., *Helianthus* sp., *Lepidospartum squamatum, Senecio* sp. BORAGINACEAE: *Cryptantha* sp. EUPHORBIACEAE: *Croton californicum, Euphorbia* sp. FABACEAE: *Cercidium* sp., *C. peninsulare, Lotus* spp. (5), *Lupinus* sp., *Phaseolus wrightii, Prosopis glan-*

*dulosa torreyana, P. velutina, Psorothamnus californica, P. fremontii.* GENTIANACEAE: *Swertia perryi.* GERANIACEAE: *Geranium* sp. HYDROPHYLLACEAE: *Eriodictyon* sp., *Phacelia ramosissima.* LAMIACEAE: *Marrubium vulgare.* LILIACEAE: *Calochortus splendens.* LOASACEAE: *Mentzelia* sp., *M. laevicaulis*. NYCTAGINACEAE: *Allionia* sp., *Boerhavia spicata.* POLEMONIACEAE: *Gilia* sp. POLYGONACEAE: *Eriogonum* spp. (4). RANUNCULACEAE: *Clematis drummondii.* SAPINDACEAE: *Sapindus* sp. SCROPHULARIACEAE: *Cordylanthus* sp., *C. filifolius, C. nevinii, C. rigidus.* ZYGOPHYLLACEAE: *Larrea tridentata.*

This is mainly a late summer- and fall-flying species. *Leucospis affinis* Say (Leucospidae) has been recorded as a parasite (Hurd, 1979).

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# CONTRIBUTIONS IN SCIENCE

## A NEW MIOCENE ENALIARCTINE PINNIPED OF THE GENUS *PTERONARCTOS* (MAMMALIA: OTARIIDAE) FROM THE ASTORIA FORMATION, OREGON

LAWRENCE G. BARNES

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# A NEW MIOCENE ENALIARCTINE PINNIPED OF THE GENUS *PTERONARCTOS* (MAMMALIA: OTARIIDAE) FROM THE ASTORIA FORMATION, OREGON

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LAWRENCE G. BARNES[1]

**ABSTRACT.** The eastern North Pacific fossil otariid pinniped genus *Pteronarctos* Barnes, 1989, includes the geologically youngest known species in the subfamily Enaliarctinae and is close to the ancestry of modern sea lions and fur seals of the otariid subfamily Otariinae. The type species of *Pteronarctos, P. goedertae* Barnes, 1989, known only from the basal part of the late Early Miocene to early Middle Miocene age Astoria Formation in coastal Oregon, is late Early Miocene in age (*circa* 19 million years old). Recently discovered fossil crania from higher in the same formation document a new species of *Pteronarctos, P. piersoni,* of early Middle Miocene age (*circa* 16 million years old). Because *Pteronarctos piersoni* has more primitive cranial morphology than the earlier *P. goedertae,* it could not have evolved from the latter species. There must be at least two lineages of *Pteronarctos* represented by fossils in the Astoria Formation, and the genus must have had a significant prior evolutionary history.

## INTRODUCTION

Fossiliferous outcrops of Tertiary marine sediments along the central Oregon coast continue to yield important new pinniped fossils. From such deposits, I have described the late Early Miocene *Pteronarctos goedertae* as a new genus and species of derived enaliarctine pinniped, a member of the family Otariidae, apparently near the ancestry of modern fur seals and sea lions of the subfamily Otariinae (Barnes, 1989). This discovery modified previous ideas (see Repenning and Tedford, 1977; Barnes, 1979) that the geochronologically older earliest Miocene (24 to 25 million years (Ma) old) *Enaliarctos mealsi* Mitchell and Tedford, 1973, from southern California was a likely ancestor of the otariines. The fossil cranium of *Pteronarctos goedertae* was discovered in strata about 19 Ma old near the base of the Astoria Formation near Newport, Oregon. This was the first pinniped taxon to have been named from coastal Oregon since Condon (1906) described *Desmatophoca oregonensis.*

The otariid subfamily Enaliarctinae, to which I assigned *Pteronarctos,* was originally named to contain *Enaliarctos mealsi* from Kern County, California. Other specimens and taxa of enaliarctines were subsequently described (Barnes, 1979), but prior to the discovery of *Pteronarctos goedertae* from coastal Oregon, the entire published record of the subfamily had been based on California fossils, principally on specimens from the earliest Miocene age Pyramid Hill Sand Member of the Jewett Sand in Kern County (Mitchell and Tedford, 1973; Barnes, 1979). For a review of my classification of otariid pinnipeds, the reader is referred to Barnes (1989).

The present article describes recently acquired fossil crania from coastal Oregon that represent a second species of *Pteronarctos, P. piersoni,* new species. These fossils were discovered at a higher stratigraphic level in the Astoria Formation and at a locality farther north along the coast than the type locality of *P. goedertae.* The new species is from the early Middle Miocene part of the Astoria Formation, *circa* 16 Ma. Because the new species and *P. goedertae* are based on virtually complete crania, all known characters used to define the two species are directly comparable.

## METHODS AND MATERIALS

Both crania of *Pteronarctos piersoni* were found in indurated calcareous sandstone concretions. The bulk of the matrix was removed from both specimens using rock-cutting saws and pneumatic chisels. Fine surface preparation was accomplished by removing the last remaining matrix from the bone using formic acid. When laboratory preparation revealed all of the critical structures in the left orbit of each specimen, it was decided not to remove the matrix filling the right orbit.

Anatomical terminology used here is adapted from that of Howell (1928), Miller, Christensen, and Evans (1964), Mitchell (1966, 1968), Hershkovitz (1971), Mitchell and Tedford (1973), Barnes (1972, 1979), and Repenning and Tedford (1977). Character polarity (primitive versus derived) was determined based on comparisons using primitive or generalized fissiped carnivores (especially canids

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[1] Curator and Section Head, Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

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and amphicynodontine ursids) as outgroups. Indications of what are commonly considered to be derived cranial characters among otariids may be obtained by consulting Howell (1928), Mitchell and Tedford (1973), Tedford (1976), Repenning and Tedford (1977), and Barnes (1979, 1989).

The suture ages of crania, calculated following the methods of Sivertsen (1954), are relative ages and not necessarily the same as ages in years. To determine a suture age, the extent of ontogenetic closure of each of nine cranial sutures is rather subjectively graded on a scale of 1 to 4 (from open to completely closed), then the scores of these nine sutures are added together to yield a relative individual age. This method is useful for comparing the relative individual ages of specimens for which teeth have not been sectioned to reveal annual growth layers.

I have identified which cranial measurements in Table 1 are the same as those that were defined by Sivertsen (1954:18–20) by appending to them the numbers that were given them by Sivertsen. Other measurements are as defined by Barnes (1972:fig.1; 1979:4–5). Crushing of the paratype cranium necessitated omitting some measurements in Table 1.

Geologic ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979), following the revised radiometric scale of Dalrymple (1979) and the correlations proposed by Armentrout (1981). Millions of years is abbreviated Ma. The acronym LACM is for the Natural History Museum of Los Angeles County, Los Angeles, California.

The crania were coated with a sublimate of ammonium chloride for photography. Cranial restorations are based primarily on the holotype of *P. piersoni*, supplemented by the paratype. The braincase of the holotype cranium is crushed by a few mm dorsoventrally, and the restorations (Figs. 3, 6, 9) compensate for this. Anatomical abbreviations in the illustrations are as follows:

ac—alisphenoid canal (posterior aperture)
at—auditory tube (= musculotubular canal, including Eustachian tube)
Bo—basioccipital
Bs—basisphenoid
cc—carotid canal
eam—external acoustic meatus
fh—hypoglossal foramen
fi—incisive foramen (= palatine fissure)
fio—infraorbital foramen
fl—lacrimal foramen
fla—anterior lacerate foramen (joined with foramen rotundum as an orbital fissure)
flp—posterior lacerate foramen
fo—foramen ovale
fop—optic foramen
fpal—palatine foramen
fpg—postglenoid foramen
Fr—frontal
fs—sphenopalatine foramen
fsm—stylomastoid foramen
g—glenoid fossa
hf—tympanohyal pit (= hyoid fossa)
Ju—jugal
mp—mastoid process
Mx—maxilla
Na—nasal
nf—nasolabialis fossa
Oc—occipital
occ—occipital condyle
Pa—parietal
Pal—palatine
Pmx—premaxilla
pp—paroccipital (= jugular) process
Ps—presphenoid
Pt—pterygoid
sop—supraorbital process
sp—fossa corresponding to pseudosylvian sulcus of brain
Sq—squamosal
tb—tympanic bulla

## SYSTEMATICS

### Class Mammalia Linnaeus, 1758
### Order Carnivora Bowdich, 1821
### Infraorder Arctoidea Flower, 1869
### Parvorder Ursida Tedford, 1976
### Family Otariidae Gill, 1866
### Subfamily Enaliarctinae Mitchell and Tedford, 1973

### *Pteronarctos* Barnes, 1989

**TYPE SPECIES.** *Pteronarctos goedertae* Barnes, 1989.

**INCLUDED SPECIES.** *Pteronarctos goedertae* Barnes, 1989, late Early Miocene, Oregon; and *P. piersoni*, new species, early Middle Miocene, Oregon.

### ***Pteronarctos piersoni*, new species**

Figures 1–9, 10a, 11a, 12a

**DIAGNOSIS OF SPECIES.** A species of *Pteronarctos* differing from *P. goedertae* by having cranium with rostrum deeper dorsoventrally, nasolabialis fossa deeper and more distinct, anterior ends of nasal bones less deeply emarginated (= more concave), dorsal surface of rostrum anteroventrally sloping, ascending (nasal) process of premaxilla shorter and transversely broader, infraorbital foramen of larger diameter, zygomatic arch more bowed dorsally, pterygoid process of palatine smaller, bony palate shorter, auditory region (including tympanic bulla and petrosal) located farther posteriorly on basicranium (indicated by styliform process of bulla, lateral to anterior end of auditory tube, extending only as far anteriorly as the anterior border of the postglenoid process), tympanic bulla smaller, mastoid process relatively thicker anteroposteriorly, crest between mastoid process and paroccipital process thicker, occipital condyles projecting farther and more prominently from occipital shield, canine crown more vertically oriented, cheek tooth rows more laterally bowed, and posterior root of M[1] distinctly bilobed instead of nearly circular.

**HOLOTYPE.** LACM 127972, complete cranium with canines, collected by Guy E. Pierson, 2 April 1983.

**TYPE LOCALITY.** LACM 4851, among loose boulders on Moolack Beach between the mouths of Schooner Creek and Moolack Creek, Lincoln County, Oregon. (Moolack is the locally used spelling of the names of both the beach and the creek, although both are shown as Moloch on the U.S. Geological Survey, Yaquina, Oregon, 15 minute topographic map, 1959 edition.)

**PARATYPE.** LACM 128002, complete cranium with left P$^4$; from LACM locality 4850, found among loose boulders on the beach on the north flank of Schooner Point, just north of the mouth of Schooner Creek, Lincoln County, Oregon; collected by Guy E. Pierson, 11 November 1985.

**FORMATION AND AGE.** The strata that yielded both the holotype and paratype of *Pteronarctos piersoni* are part of a stratigraphic section that has been referred to the Astoria Formation and are early Middle Miocene in age and approximately 16 Ma old. They represent the Newportian Molluscan Stage and are correlated with the Hemingfordian North American Land Mammal Age.

The name Astoria Formation was originally proposed for late Early Miocene rocks exposed farther north, at Astoria, Oregon, on the south side of the Columbia River, and the formation name has been subsequently applied to the slightly younger strata of late Early Miocene to early Middle Miocene age that were deposited in the Newport Embayment along the coast of Oregon (Howe, 1926; Packard and Kellogg, 1934; Ray, 1976:fig. 2; Colbath, 1985: 849). The Astoria Formation is the only Tertiary age rock unit that crops out in the sea cliffs at Moolack Beach at the collecting localities of the holotype and paratype. The geology of this area has been discussed by Schenck (1928), Packard and Kellogg (1934:4–7), Moore (1964), and Colbath (1985). The locality where Colbath (1985) studied molluscan paleoecology is approximately 4 km north of the localities that produced *P. piersoni.*

Both specimens of *P. piersoni* were found in rounded, extremely hard, fine-grained gray concretions that typically weather out of the sea cliff at Moolack Beach from an easily recognizable concretionary horizon in the Astoria Formation that has become known as the "Iron Mountain bed" (see Munthe and Coombs, 1979:78–79; Armentrout, 1981:141 (note 29)).

The entire thickness of the Astoria Formation and its contained molluscan fauna at this part of the Oregon coast were used by Addicott (1976:102, 104, fig. 4) to characterize the Newportian Molluscan Stage (and see Armentrout, 1981). This stage, correlated with the early part of the "Temblor" provisional provincial mega-invertebrate stage as characterized by Addicott (1972) on the basis of Californian fossils and the Saucesian foraminiferal stage (Addicott, 1976; and see Moore, 1964:20–21), has also been correlated with the Hemingfordian North American Land Mammal Age and the Burdigalian Stage of Europe (see Barnes, 1989:8, and references cited therein). The same "Iron Mountain bed" that yielded the *Pteronarctos piersoni* fossils also produced the cranium of the dome-headed Hemingfordian chalicothere, *Tylocephalonyx* sp., described by Coombs (1979) and Munthe and Coombs (1979) and estimated in the latter reference to be between 15 and 16 Ma old. The Depoe Bay Basalt, which unconformably overlies and intrudes the Astoria Formation in this area, has yielded dates originally published as 15.2 ± 0.6 Ma, 14.5 ± 1.0 Ma, and 14.0 ± 2.7 Ma (Turner, 1970; and see Munthe and Coombs, 1979). When these dates are corrected using the factors supplied by Dalrymple (1979), the age of the Depoe Bay Basalt is still calculated at about 14.4 to 15.6 Ma, and these dates would postdate deposition of the uppermost part of the Astoria Formation. The age of the base of this section of the Astoria Formation is more difficult to estimate. Armentrout (1981:139) placed the lower boundary of the Newportian Stage (and therefore of the Astoria Formation in this area) at approximately 20 Ma. The Oregon coastal section of the Astoria Formation therefore spans from approximately 15 to 20 Ma (see Ray, 1976:fig. 2; Repenning and Tedford, 1977:table 1; Munthe and Coombs, 1979:78–79; Armentrout, 1981; Barnes, 1989). Because the holotype and paratype of *P. piersoni* are from a horizon that is stratigraphically high within the stratotype of the Newportian Stage, the age of these specimens is undoubtedly coincident with the younger parts of all of the above ages and is estimated at 16 Ma.

**ETYMOLOGY.** The species is named in honor of Mr. Guy E. Pierson of South Beach, Oregon, who collected both the holotype and paratype.

**DESCRIPTION AND COMPARISONS.** The cranium of *Pteronarctos goedertae* has been described, illustrated, and compared with those of other enaliarctines (Barnes, 1989). It is unnecessary to duplicate here the description of cranial anatomy that is identical in *P. goedertae* and the previously described enaliarctines. Therefore, I will describe the characters that differentiate *P. piersoni* from related taxa and interpret the similarities and differences.

The holotype apparently represents a young adult male (Group I of Sivertsen (1954)) based on the following observations: (1) the only cranial suture that is obliterated by fusion is the occipito-parietal, all other sutures are unfused and are readily visible because of matrix that fills them; (2) the cranium yields a suture age of at least 23 (see Table 2) by employing the methodology of Sivertsen (1954), thus placing it in the adult age class; (3) as in Recent adult male otariines, a sagittal crest is present; and (4) the canines are fully erupted but not heavily worn, with only slight wear on the apex of the right one.

The paratype apparently represents a slightly older adult male than the holotype (Group I of Sivertsen) based on the following observations: (1) suture fusion is more advanced than in the holotype, four cranial sutures are obliterated by fusion (the occipito-parietal, coronal, basioccipital-basiphenoid, and maxillary), the interparietal and premaxillary-maxillary sutures are comparatively more closed, and all other sutures are unfused and are readily visible

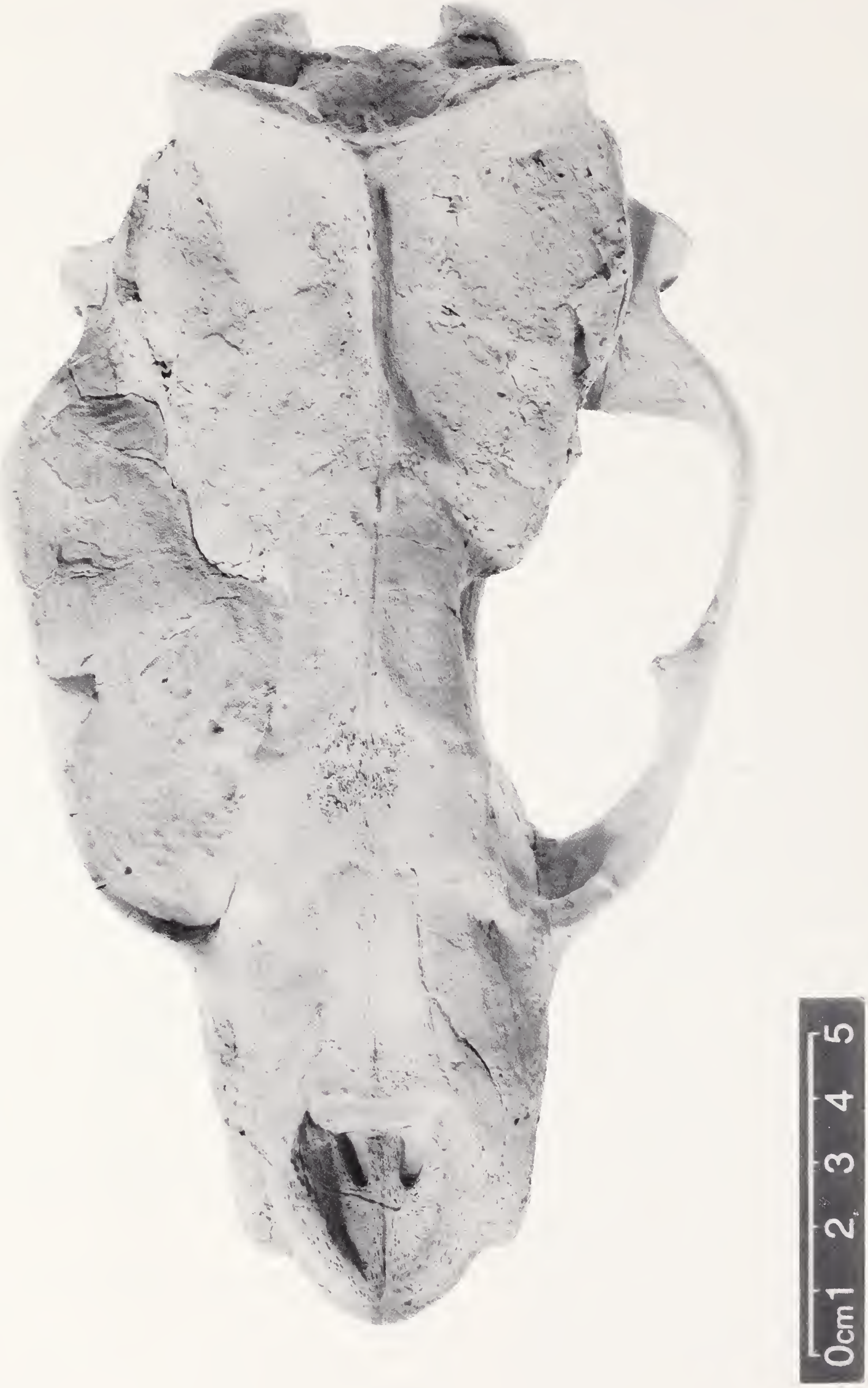

Figure 1. *Pteronarctos piersoni*, new species, holotype cranium, LACM 127972, from LACM locality 4851, dorsal view.

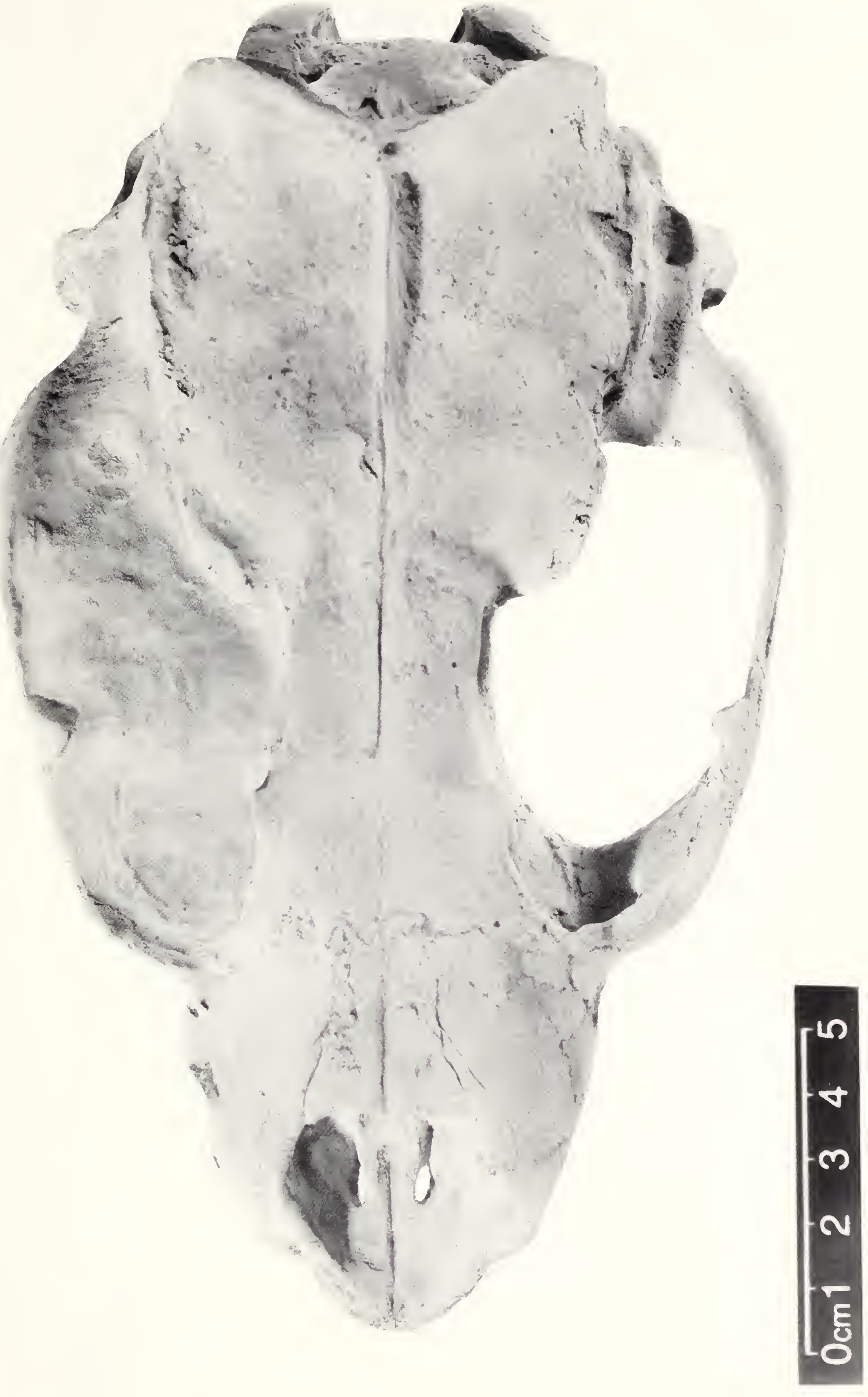

**Figure 2.** *Pteronarctos piersoni*, new species, paratype cranium, LACM 128002, from LACM locality 4850, dorsal view.

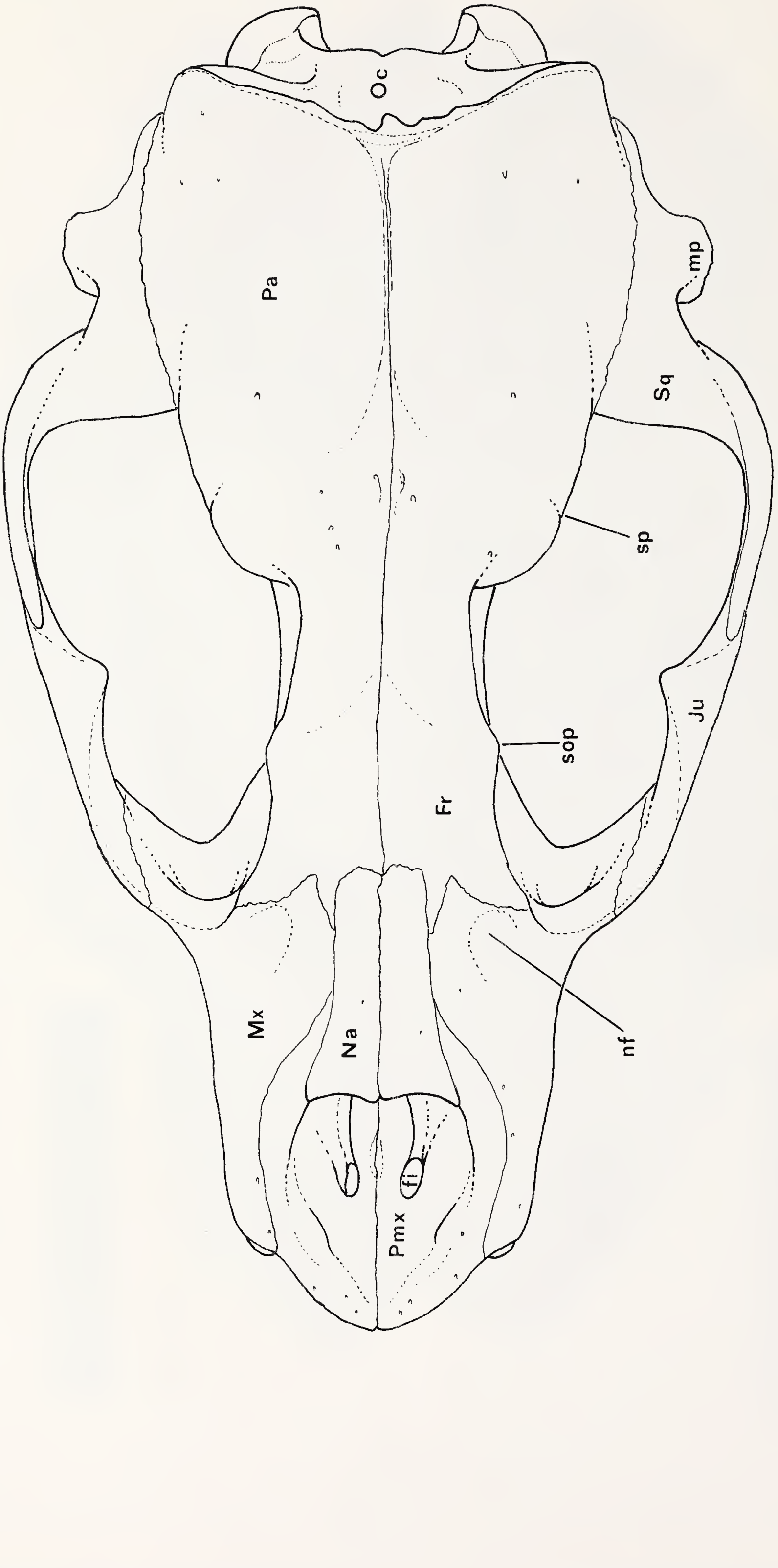

**Figure 3.** *Pteronarctos piersoni,* new species, restoration of cranium based on holotype and paratype, dorsal view; for explanation of abbreviations see Methods and Materials.

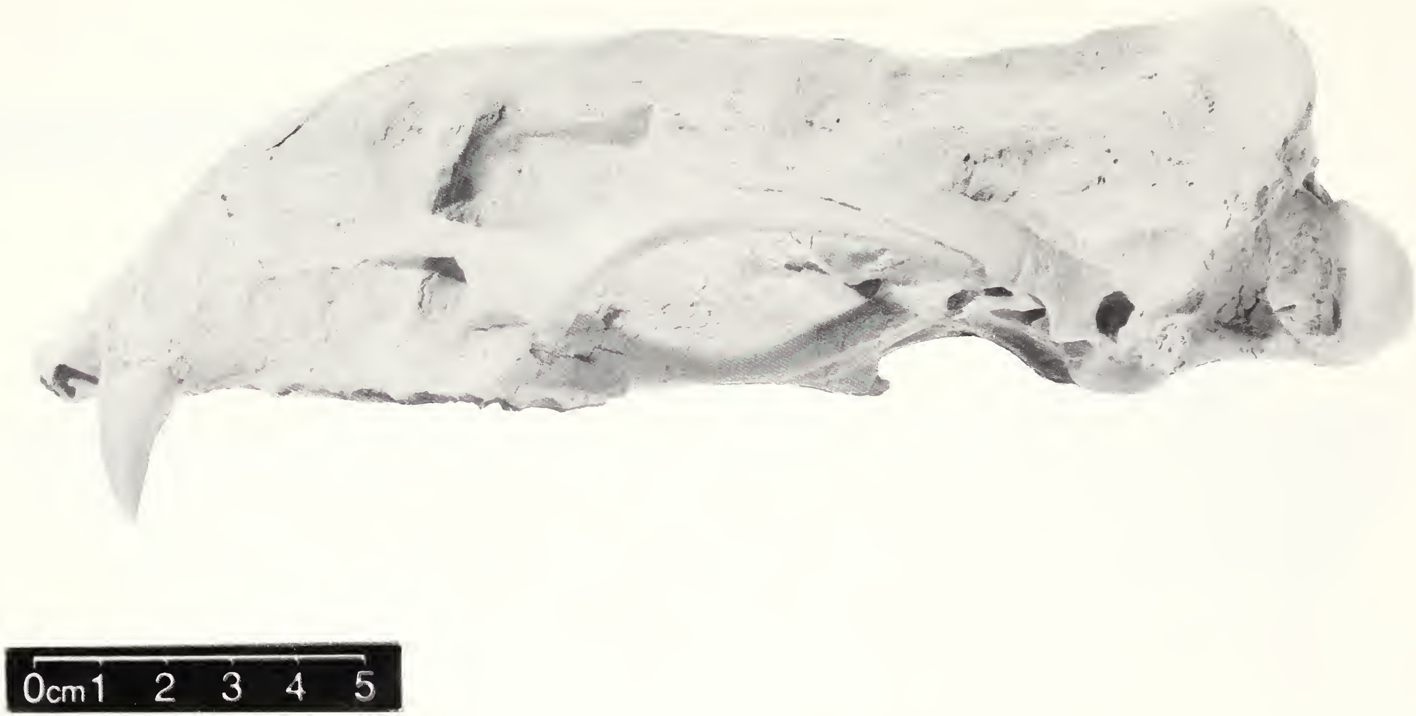

**Figure 4.** *Pteronarctos piersoni*, new species, holotype cranium, LACM 127972, from LACM locality 4851, left lateral view.

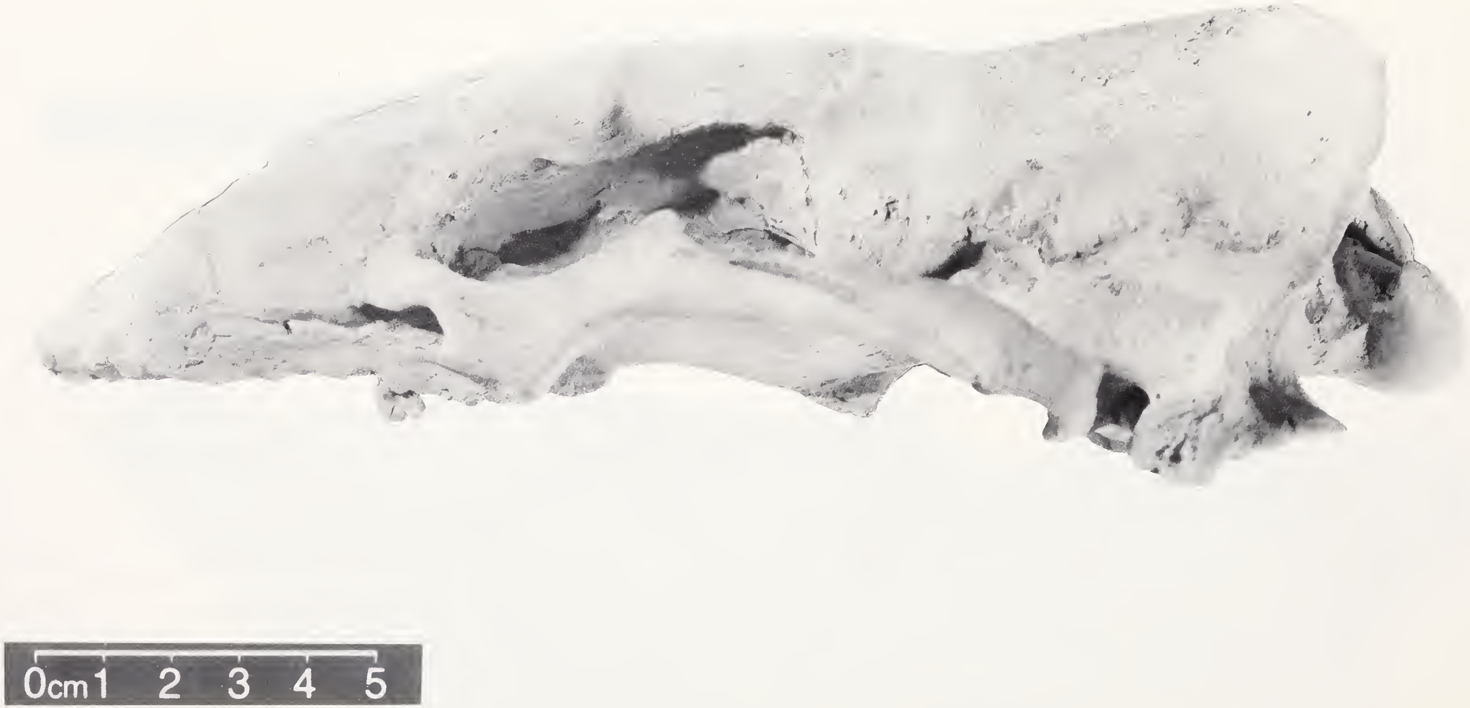

**Figure 5.** *Pteronarctos piersoni*, new species, paratype cranium, LACM 128002, from LACM locality 4850, left lateral view.

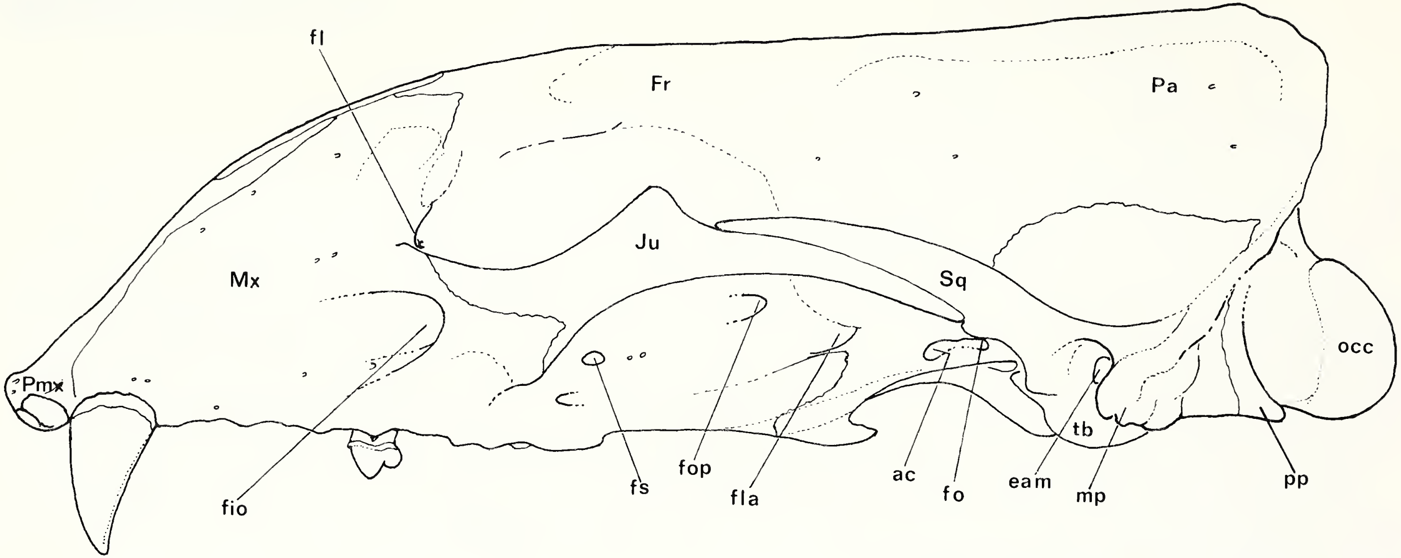

Figure 6. *Pteronarctos piersoni*, new species, restoration of cranium based on holotype and paratype, left lateral view; for explanation of abbreviations see Methods and Materials.

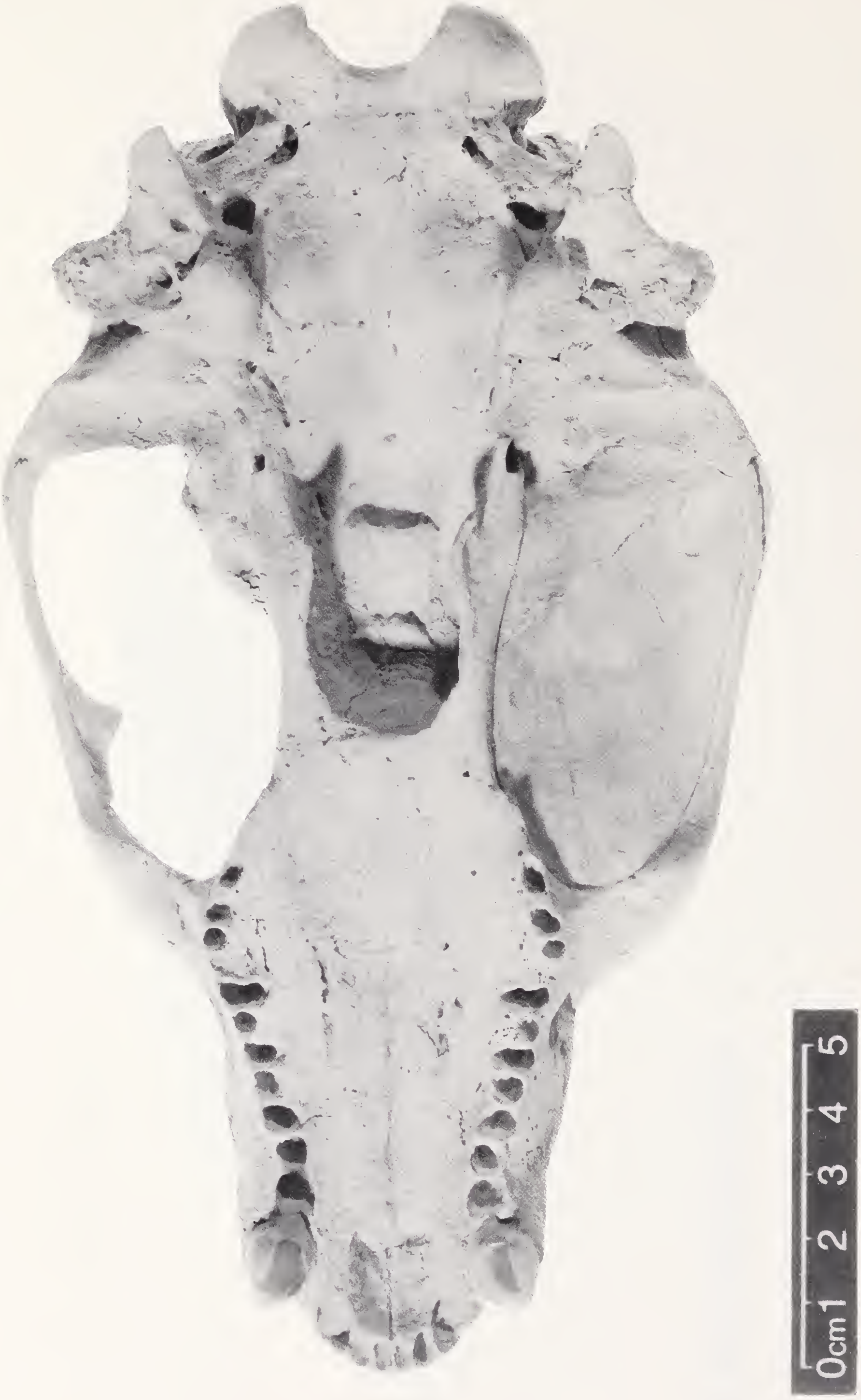

Figure 7. *Pteronarctos piersoni*, new species, holotype cranium, LACM 127972, from LACM locality 4851, ventral view.

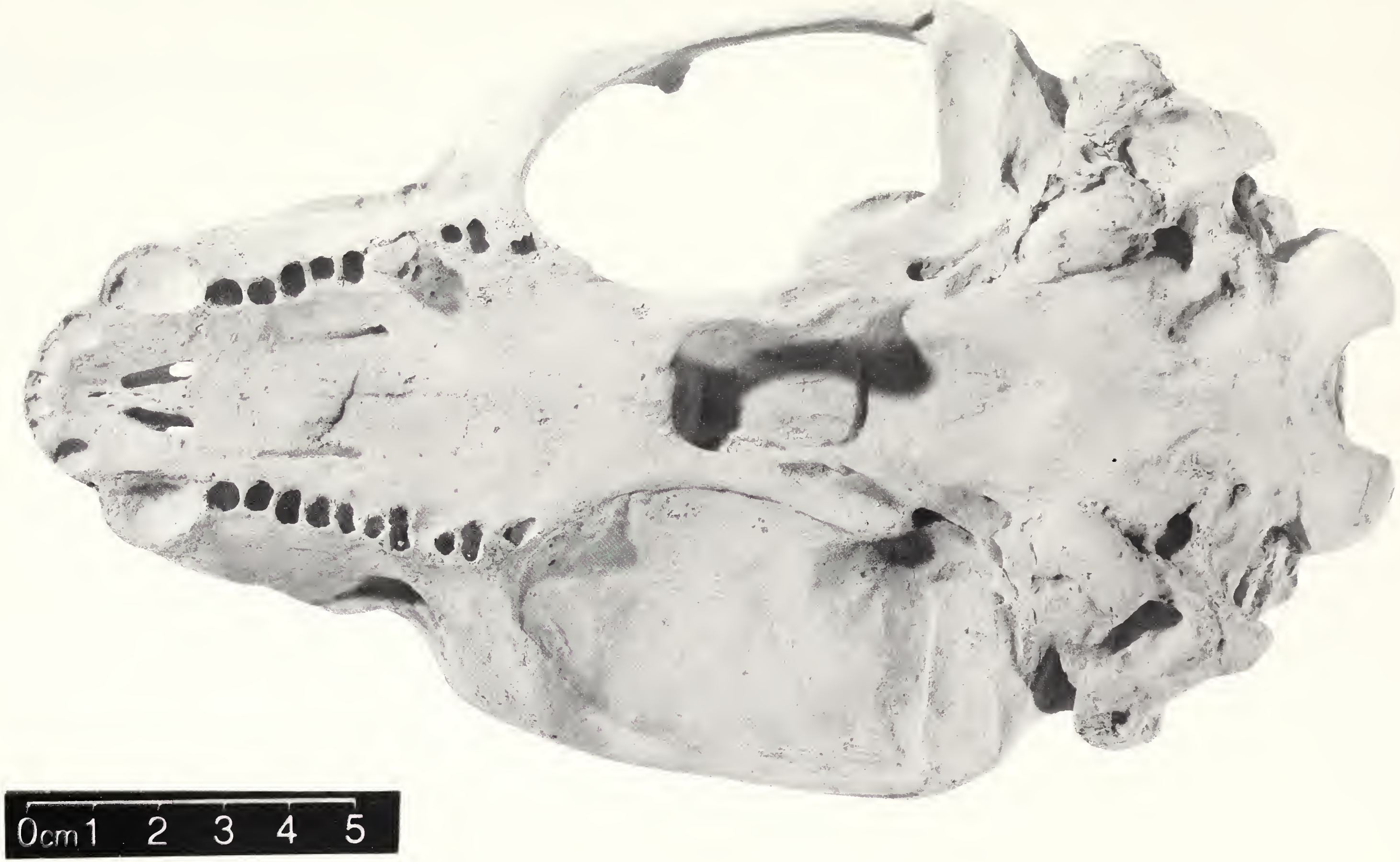

Figure 8. *Pteronarctos piersoni*, new species, paratype cranium, LACM 128002, from LACM locality 4850, ventral view.

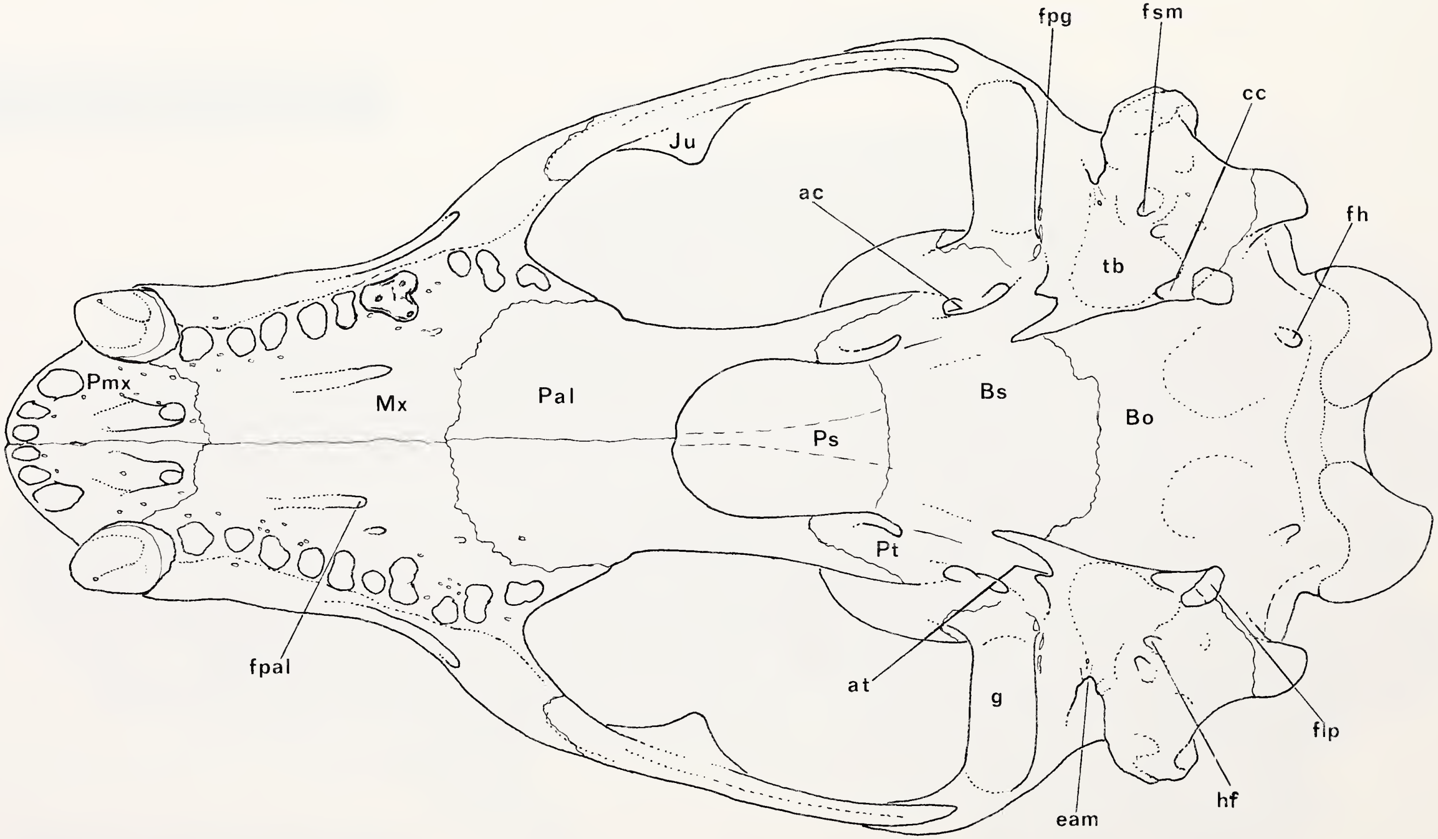

**Figure 9.** *Pteronarctos piersoni*, new species, restoration of cranium based on holotype and paratype, ventral view; for explanation of abbreviations see Methods and Materials.

**Table 1. Measurements (in mm) of crania of *Pteronarctos piersoni,* new species. See Methods and Materials section for methods of measurements.**

| | Holotype LACM 127972 | Paratype LACM 128002 |
|---|---|---|
| Total length (condylobasal length) (0) | 212.5 | 212.2 |
| Post-palatal length (palatal notch to basion) | 102.5 | 101.2 |
| Basion to anterior edge of zygomatic root (18) | 142.0 | 142.2 |
| Length of tooth row, C to $M^2$ | 70.7 | 69.1 |
| Width of rostrum across canines (12) | 47.2 | 47.6 |
| Width of palate across anterior alveoli of $P^4$ | 48.4 | 47.6 |
| Width between infraorbital foramina | 50.2 | — |
| Width across antorbital processes (5) | 47.8 | — |
| Width across greatest interorbital constriction (6) | 36.5 | 38.0 |
| Width across supraorbital processes (7) | 37.0 | 39.2 |
| Width across greatest intertemporal constriction | 26.6 | 29.1 |
| Width of braincase at anterior edge of glenoid fossa (8) | 68.1 | 67.9 |
| Zygomatic width (17) | 121.8 | 124.8 |
| Auditory width (19) | 93.4 | 96.8 |
| Mastoid width (20) | 103.8 | 109.0 |
| Paroccipital width | 79.0 | 86.2 |
| Greatest width across occipital condyles | 52.1 | 51.3 |
| Greatest width of anterior nares | 25.2 | — |
| Greatest height of anterior nares | 26.6 | — |
| Width of zygomatic root of maxilla (14) | 13.0 | 13.6 |
| Greatest width of foramen magnum | 26.1 | 23.6 |
| Greatest height of foramen magnum | 16.0 | 15.1 |
| Transverse diameter of infraorbital foramen | 8.4 | 7.4 |

because of matrix that fills them; (2) the cranium yields a suture age of at least 30 (see Table 2) by employing the methodology of Sivertsen (1954), thus placing it in the adult age class; (3) a sagittal crest is present; and (4) the left $P^4$ shows moderate wear.

I have suggested (Barnes, 1979:16) that species of *Enaliarctos* were sexually dimorphic, with females having canines that are 20 to 32 percent smaller than those of males. The canines of the holotype of *P. piersoni* are nearly equal in size to those attributed to male (= the larger dimorph) *Enaliarctos* sp. from near the type locality of *E. mealsi.* Additionally, both the holotype and paratype crania of *P. piersoni* are approximately the same size and have canines (or canine alveoli) equal in size to those of the holotype of *P. goedertae,* which was interpreted as being from a male (see Barnes, 1989).

Both crania apparently indicate the typical skull size for mature males of the species. Even though the paratype cranium demonstrates a significantly more advanced stage of suture fusion (Table 2), the two crania are nearly identical in size and proportions (Table 1).

Both known crania of *P. piersoni* are virtually complete, but the holotype (LACM 127972) is the least distorted of the two. Postdepositional sediment compaction has resulted in the dorsoventral compression of the brain case of the holotype (Fig. 4) and of the rostrum and anterior part of the braincase of the paratype (LACM 128002, Fig. 5). The latter has thus undergone breakage and outward displacement of the lateral surfaces of the rostrum, the braincase, and the orbital wall. Both crania apparently underwent preburial transport that resulted in loss of teeth and slight abrasion prior to fossilization. The holotype has both canines in place, and the paratype has only the left $P^4$. All other teeth of both specimens fell out before final burial.

As with *P. goedertae,* the rostrum tapers smoothly anteriorly and the canine roots do not form prominent bulges in the cheek region. In anterior view, the widest part of the external narial opening of *P. piersoni* is at a higher point than in *P. goedertae.* The anterior narial opening is smaller in *P. piersoni* than in *P. goedertae* (Fig. 10). In contrast with *P. goedertae,* the anterior margin of each nasal bone is less concave, the rostrum is deeper and more arched (derived condition), and the nasolabialis fossa is more distinct (primitive condition). In *Pteronarctos piersoni* the ascending (nasal) process of the premaxilla is broader transversely and does not extend as far posteriorly (Fig. 10) as in *P. goedertae* (which has the primitive condition as in primitive arctoid carnivores). The suture between the maxilla and premaxilla is clearly visible on both specimens. On the holotype, the maxillary-frontal suture is visible as it trends laterally toward the orbit, between the nasolabialis fossa and the small antorbital process. In *P. piersoni,* the diameter of the infraorbital foramen is approximately 1.5 times that of the same foramen in *P. goedertae.* The larger diameter of this foramen in *P. piersoni* is a derived character. The zygomatic arch is more bowed dorsally at midpoint in *P. piersoni* than in *P. goedertae,* and this is a more primitive character.

The posterior part of the interorbital region is more constricted in the holotype of *P. piersoni* than in the paratype, and such differences are characteristic of the variability within Recent otariine species (see King, 1954:table 1 for *Arctocephalus australis;* Orr, Schonewald, and Kenyon, 1970:table 3 for *Zalophus californianus;* and Itoo, 1985: table 1 for *Zalophus californianus japonicus*). Although both known crania of *P. piersoni* have low sagittal crests on the braincase, neither has an anterior extension of this crest over the interorbital area, a derived condition that exists in *P. goedertae.*

Both the holotype and paratype have undergone breakage of the braincase along the parietal-squamosal suture, and this suture can be traced on both specimens and is shown in the restorations (Figs. 3, 6). The nuchal crests on both crania of *P. piersoni* are broader and not directed so far posteriorly as they are in *P. goedertae* (which has the primitive condition). In *P. piersoni* the occipital condyles project farther posteriorly than they do in *P. goedertae.* They are set off from the occipital shield more prominently (primitive condition), and they are thus visible extending beyond the nuchal crest in dorsal view (see Figs. 1–3).

The holotype has the typically flat palate of *Pteronarctos,* although the palate of the paratype has been distorted by sediment compaction and its slight arch is an artifact of preservation. All of the palatal sutures shown in Figure 9, including the pterygoid-palatine sutures, are observable on the holotype. The paratype has two very distinct palatine foramina that continue anteriorly, just as in *P. goedertae* (Fig. 8). On the holotype of *P. piersoni,* the same grooves are more shallow (Fig. 7). Located at the posterior margin of the palate ventral to the orbit, the pterygoid process is smaller than in *P. goedertae* (Figs. 12a, b), a more primitive condition. The bony palate is shorter in *P. piersoni* than in *P. goedertae,* so that the internal narial opening is 6 to 7 mm farther anterior on the cranium relative to the anterior end of the zygomatic arch. Concomitant with the shorter palate of *P. piersoni* is a longer pterygoid-palatine strut.

The canines of the holotype of *P. piersoni* are virtually the same size and have the same morphology as those of the holotype of *P. goedertae.* However, in *P. piersoni* the canine crowns are more vertically oriented relative to the plane of the palate (more primitive condition, see Figs. 11a, b). The locations, sizes, and shapes of the alveoli for $P^{1-4}$ are virtually identical to those of *P. goedertae.* In contrast with the condition in *P. goedertae,* the cheek tooth row of *P. piersoni* is more bowed laterally in the region of the $P^4$ and $M^1$ (Figs. 12a, b; primitive condition).

A left $P^4$ remains in the paratype cranium (Figs. 5, 8), and this is the first cheek tooth positively identified for the genus. (Barnes (1989) described an isolated $M^1$ from California that had the appropriate root morphology for *P. goedertae.*) The crown of the $P^4$ of *P. piersoni* is nearly an equilateral triangle in occlusal view (Fig. 9). The paracone is the major cusp and is broad anteroposteriorly and transversely compressed. It lies near the lateral part of the crown, and the smaller metacone lies directly posterior to it. An undulating labial cingulum (Fig. 6) curves apically around both the anterior and posterior ends of the crown to produce, at each location, a small cusp. The protocone is reduced to a low cusp separated from the paracone by a trigon basin and bordered lingually by a cingulum that is confluent with the labial cingulum. The tooth is less sectorial than is the homologous carnassial in *Enaliarctos mealsi,* and this is consistent with the cheek dentition of *Pteronarctos* being more nearly homodont than that of *Enaliarctos.* In comparison with the (more primitive) $P^4$ of *E. mealsi,* the metacone in *P. piersoni* is much smaller and has moved more anteriorly, and the protocone has moved more posteriorly relative to the paracone. As in *P. goedertae,* the anterior root above the paracone remains separate, and the posterior root above the metacone has merged with the medial one above the protocone to form a single bilobed root. In size and shape, the $P^4$ of *P. piersoni* is very similar to the $P^4$ in the holotype cranium of the Early Miocene enaliarctine *Pinnarctidion bishopi* Barnes, 1979. On the $P^4$ of *Pteronarctos piersoni,* the protocone is slightly higher, the labial margin is slightly bowed lingually, and the posterior margin of the crown, posterior to the trigon basin, is more concave. The overall aspect of the $P^4$ of *P. piersoni* shows a tooth form that is more like the anterior premolars, with the paracone becoming the principal cusp, in a cheek tooth row that is in the process of achieving homodonty.

**Table 2. Degree of closure of sutures and suture ages of crania of *Pteronarctos piersoni,* new species. Suture nomenclature, numbers, and methods follow Sivertsen (1954).**

| | Holotype LACM 127972 | Paratype LACM 128002 |
|---|---|---|
| I. Occipito-parietal | 4 | 4 |
| II. Squamoso-parietal | 3 | 3 |
| III. Interparietal | 2 | 3 |
| IV. Interfrontal | 2 | 2 |
| V. Coronal | 3 | 4 |
| VI. Basioccipito-basisphenoid | 2 | 4 |
| VII. Maxillary | 2 | 4 |
| VIII. Basisphenoid-presphenoid | 3 | 3 |
| IX. Premaxillary-maxillary | 2 | 3 |
| Total (suture age) | 23 | 30 |

The $M^1$ of *P. piersoni* has differently configured roots than that of *P. goedertae.* In *P. goedertae,* the posterior root is elongate anteroposteriorly, the elongation reflecting two originally separate roots, one above the protocone and one above the metacone. In *P. piersoni,* this same double posterior root is much more distinctly bilobed, and the elongation is oriented obliquely to the sagittal plane (Figs. 12a, b), a more primitive condition.

The basioccipital-basisphenoid suture is most distinct on the holotype, whereas the basisphenoid-presphenoid suture and the presphenoid-pterygoid sutures are most distinct on the paratype. The entire auditory region of *P. piersoni* is positioned on the basicranium in a location that is typical of otariids and generalized fissipeds (the primitive condition).

Only the styliform process of the tympanic bulla projects farther anteriorly than the anterior surface of the postglenoid process. This is in contrast to the relatively unusual and derived condition in *P. goedertae,* in which the entire ear region is positioned more anteriorly on the basicranium, and the anterior part of the tympanic bulla, ventral to the auditory tube, extends anteromedial to the postglenoid process. In *P. goedertae,* the tympanic bullae are broad and most inflated in their centers. In contrast, the bullae on both crania of *P. piersoni* are relatively smaller and most inflated in their medial parts. On the holotype cranium, the most inflated part of each bulla bulges medially toward the basioccipital, whereas neither bulla of the paratype bulges in this fashion, and the inflated part of each bulla is aligned anteroposteriorly. Similar variation in bullae exists among samples of Recent species of Otariinae.

On both crania of *P. piersoni,* the mastoid process is thicker anteroposteriorly than in *P. goedertae,* and the crest of bone that joins the mastoid process with the paroccipital process is also thicker (derived condition) than it is in *P. goedertae.* In *P. goedertae,* the lateral margin of this crest is nearly straight between the two processes, whereas in *P. piersoni* the margin is concave. On the holotype of *P. goedertae,* the posterior extremities of both paroccipital processes are missing, so the crania of *P. piersoni* provide the first indication of their true shapes in the genus *Pteronarctos.* These processes are relatively broad, and their laterally bowed lateral margins give them the appearance of bending medially at the posterior ends. On both the holotype and paratype, the exoccipital-squamosal suture is visible as it extends across the lateral surface of the paroccipital process (Fig. 6), thence on the ventral surface of the process to the posterolateral side of the posterior lacerate foramen (Fig. 9).

## DISCUSSION AND CONCLUSIONS

*Pteronarctos piersoni* is the third named species of otariid pinniped described from the Astoria Formation in coastal Oregon. The first species was the large desmatophocine, *Desmatophoca oregonensis* Condon, 1906. Thus, members of at least two distinct subfamilies of otariid pinnipeds are found in this same stratigraphic interval of the Astoria Formation. One subfamily is represented by the *Desmatophoca* lineage, the other by the more otariine-like *Pteronarctos* lineage, and they both apparently occupied this area of coastal Oregon during early Middle Miocene time. Without more data, however, it is not possible to determine if populations of these pinnipeds lived at the site at different times of the year, because of differing seasonal migrations, or if they were truly sympatric to the point of using the same beaches on which to haul out simultaneously.

The dentition of *Pteronarctos piersoni,* based on the canines, the $P^4$, the empty alveoli for other teeth, and inferred from the known $I^3$ of *P. goedertae,* was apparently somewhat like that of Recent otariines. Although the $P^4$ retained some sectorial function, on the whole the cheek dentition was becoming homodont. *Pteronarctos piersoni* might have been able to feed on squid or crustaceans, but its main diet, like that of most Recent Otariinae, probably was mostly fish. *Desmatophoca oregonensis* has a somewhat different type of dentition, with more bulbous cheek tooth crowns. It might have also been partly or largely piscivorous, and the two species certainly could have been competing for the same type of food resources.

Although the type locality of *D. oregonensis* is near Newport, farther south along the coast and stratigraphically lower in the Astoria Formation, the only published referred cranial material of the species (see Barnes, 1987) is from the same locality and approximately the same stratigraphic horizon as the holotype of *P. piersoni.* The referred specimen of *D. oregonensis* and the holotype and paratype of *P. piersoni* are all from the 1.5 km section of Moolack Beach extending from Schooner Point, at the mouth of Schooner Creek, northward toward the mouth of Moolack Creek. A cranium referred to the cetotheriid mysticete whale, *Cophocetus oregonensis* Packard and Kellogg, 1934, and a cranium of the bizarre dome-headed chalicothere, *Tylocephalonyx* sp. (see Coombs, 1979; Munthe and Coombs, 1979), were found along the same section of Moolack Beach. These fossils are all derived from essentially the same beds, within a few meters stratigraphically of one another, relatively high in the Astoria Formation and are early Middle Miocene in age (*circa* 16 Ma).

The fossil mollusks from this part of the Astoria Formation indicate an environment of deposition in warm-temperate true marine conditions on an open shelf in shallow to moderate depths over a substrate of silty mud to fine sand (Moore, 1964: 17; Colbath, 1985:849, 867). These are the conditions in which the holotype of *P. goedertae* was buried and might have been indicative of its living environment.

The type species of *Pteronarctos, P. goedertae,* was collected from a much lower stratum, very close to the base of the Astoria Formation near Newport, Oregon, and is late Early Miocene in age. This lower part of the Astoria Formation represents the lower part of the Newportian molluscan stage and because the chalicothere found higher in the formation at Moolack Beach indicates a correlation with the Hemingfordian North American Land Mammal Age (Coombs, 1979), the age of *P. goedertae* is probably older and close to 19 Ma (Barnes, 1989).

*Pteronarctos piersoni* is therefore known only from strata that are approximately 3 Ma younger than the horizon that yielded *P. goedertae.* It is interesting and phylogenetically significant, therefore, that the chronologically younger of the two species, *P. piersoni,* has a greater number of prim-

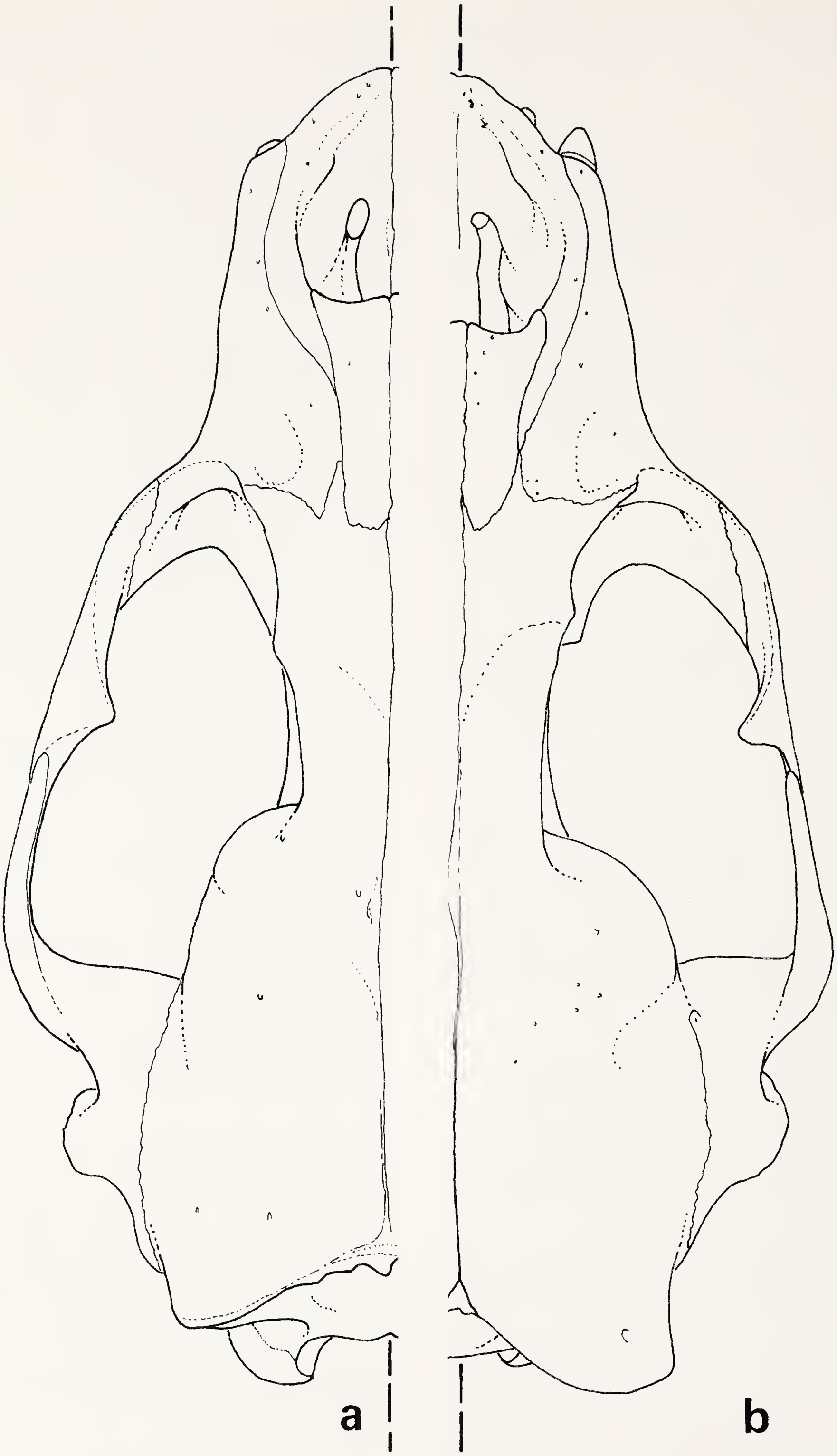

**Figure 10.** Comparative dorsal views of crania of species of *Pteronarctos;* **a,** *P. piersoni,* new species; **b,** *P. goedertae* Barnes, 1989 (after Barnes, 1989:fig. 2).

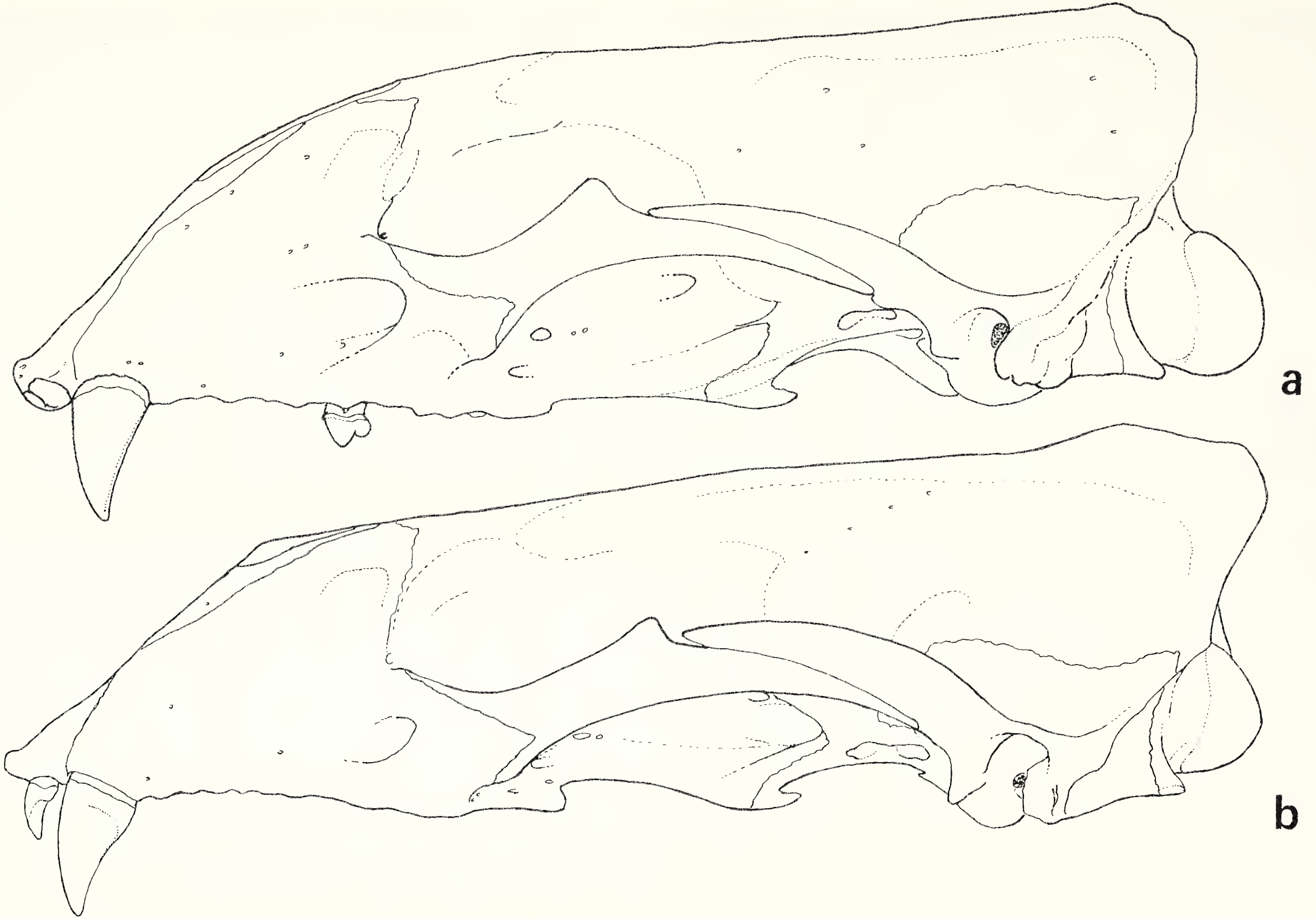

Figure 11. Comparative lateral views of crania of species of *Pteronarctos*; a, *P. piersoni*, new species; b, *P. goedertae* Barnes, 1989 (after Barnes, 1989:fig. 3b).

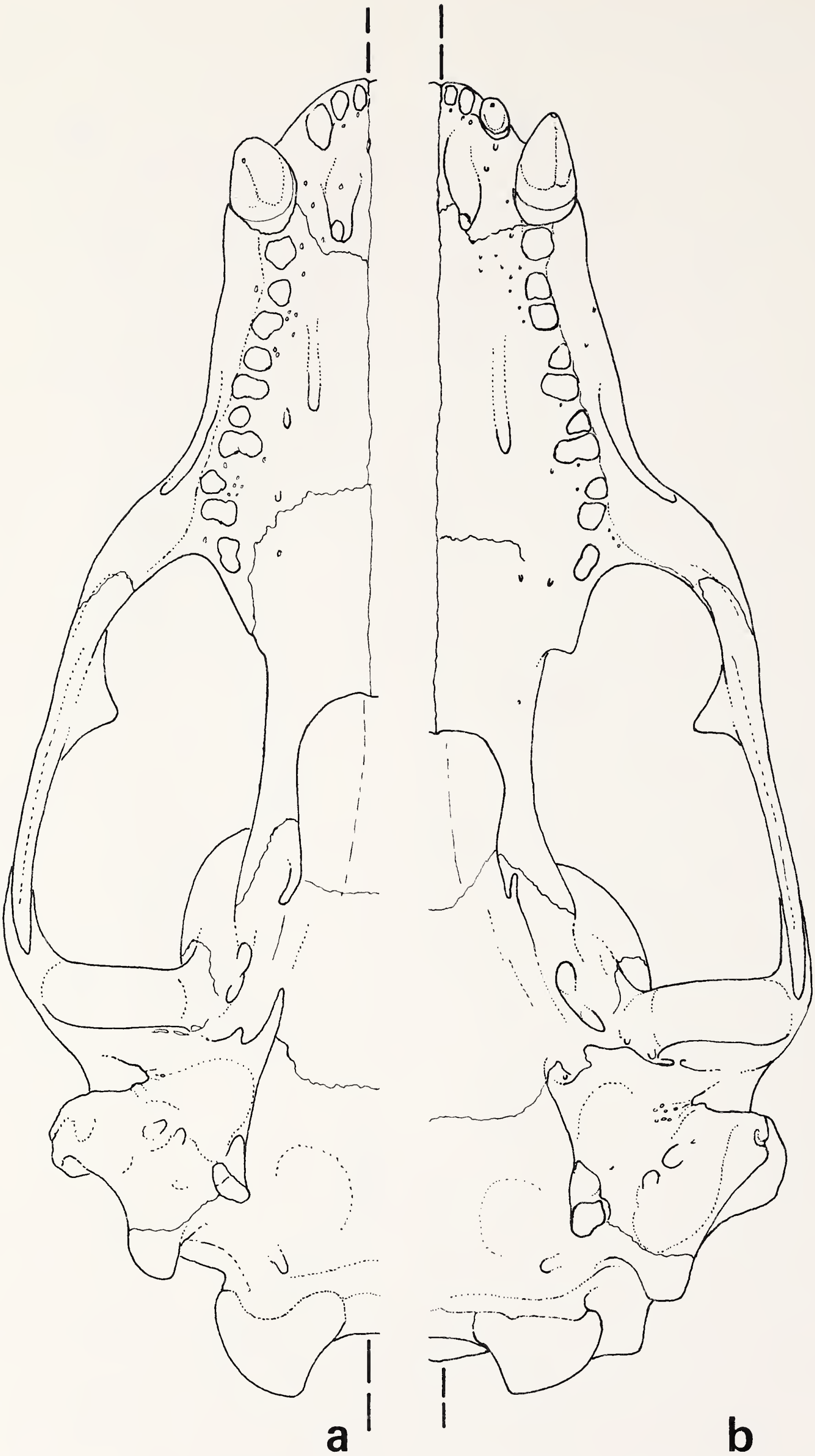

**Figure 12.** Comparative ventral views of crania of species of *Pteronarctos;* **a,** *P. piersoni,* new species; **b,** *P. goedertae* Barnes, 1989 (after Barnes, 1989:fig. 6).

itive cranial characters than *P. goedertae.* These characters are interpreted to be primitive because they are more like those of fissiped carnivores than like those of derived Otariidae. They include, but are not limited to, deeper nasolabialis fossa on the cheek, more dorsally curved zygomatic arch, smaller pterygoid process at the back of the palate, more vertically oriented canine crowns, more strongly laterally bowed cheek tooth rows, distinctly bilobed posterior root of M$^1$, shorter palate, posteriorly positioned auditory region of the basicranium, smaller tympanic bulla, and more prominently projecting occipital condyles (Figs. 10–12). *Pteronarctos piersoni* does have a few derived characters compared with *P. goedertae,* and these are the greater depth of the rostrum, shorter and broader ascending (nasal) process of the premaxilla, larger diameter of the infraorbital foramen, and less prominent and more dorsally directed nuchal crest. The interesting situation exists, therefore, that the geochronologically earlier species, *P. goedertae,* has a greater number of derived characters than the later species, *P. piersoni.*

Clearly, the most parsimonious interpretation is that the older, yet more highly derived, *P. goedertae* could not have been ancestral to the more primitive, yet chronologically younger, *P. piersoni.* This interpretation avoids invoking evolutionary reversals in several character states. The two species undoubtedly evolved from a common ancestor, and this suggests that the genus *Pteronarctos* includes more than one lineage, that at least two such lineages are represented by fossils in the Astoria Formation, and that the first appearance of the genus probably will prove to be prior to the late Early Miocene occurrence of *P. goedertae.* A parallel situation was reported by Barnes (1987) for the genus *Desmatophoca* Condon, 1906, in which the older species, *D. brachycephala* Barnes, 1987, from the Early Miocene Astoria Formation in Washington is more derived than early Middle Miocene *D. oregonensis* from the coastal Oregon exposures of the Astoria Formation. The characters differentiating *P. piersoni* from *P. goedertae* are similar in kind and magnitude to differences between Recent species of arctocephaline fur seals of the polytypic genus *Arctocephalus* (see Repenning, Peterson, and Hubbs, 1971; Bonner, 1981).

The P$^4$ of *Pteronarctos piersoni* indicates that the cheek tooth row of the species was more nearly homodont than in *Enaliarctos mealsi.* Because *P. piersoni* is in general more primitive than *P. goedertae,* the latter species retains its position as the enaliarctine that shares the greatest number of derived characters in common with the living fur seals and sea lions of the subfamily Otariinae.

It must be re-emphasized that although *Enaliarctos mealsi* is, on the whole, the most primitive species of otariid pinniped yet described, in some character states *Pteronarctos goedertae* is more primitive (e.g., a shorter posterior extension of the palate ventral to the choana, a smaller posterior lacerate foramen, a bilobed posterior root on P$^3$ representing a remnant relic of the medial (protocone) root, and a large M$^2$ alveolus; see Barnes, 1989:15). Now *P. piersoni* is known to have been yet more primitive than *P. goedertae.* The presence of these primitive characters in species of *Pteronarctos* prohibits consideration of any known species of *Enaliarctos* as being ancestral to either species of *Pteronarctos* (unless evolutionary reversals of several characters were invoked). *Pteronarctos* could share a common ancestry with *Enaliarctos,* however (see Barnes, 1989:fig. 9).

The classification of nominal species in the subfamily Enaliarctinae is summarized below. The genus *Enaliarctos* is listed first because of its preponderance of primitive characters. The subfamily Enaliarctinae, as used here, is paraphyletic (see also Berta, 1989), representing a basal group of primitive Otariidae from which several more derived lineages appear to have arisen. The diagnosis given for the subfamily in Barnes (1979) still pertains to all included species.

Family Otariidae Gill, 1866
Subfamily Enaliarctinae Mitchell and Tedford, 1973
*Enaliarctos* Mitchell and Tedford, 1973
*Enaliarctos mealsi* Mitchell and Tedford, 1973
*Enaliarctos mitchelli* Barnes, 1979
*Pteronarctos* Barnes, 1989
*Pteronarctos piersoni,* new species
*Pteronarctos goedertae* Barnes, 1989
*Pinnarctidion* Barnes, 1979
*Pinnarctidion bishopi* Barnes, 1979

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